DISTRIBUTION AND ABUNDANCE OF HYPERIID AMPHIPODS IN NEAR-SURFACE WATERS OF THE NORTH ATLANTIC OCEAN AND NORTH SEA

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A thesis submitted for the
degree of Doctor of Philosophy
to the University of Edinburgh

April 1970

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A ABSTRACT

The monthly collections of the Continuous Plankton Recorder survey provide a uniquely broad coverage of plankton distribution at the 10 m level in the North Atlantic Ocean and North Sea. Data records and original samples taken over four years are analysed for diurnal, seasonal, annual and geographical variations in the abundance and composition of hyperiid amphipods. Results are compared and discussed with reference to pertinent environmental and biological information.

Despite extensive seasonal expansion and contraction, distributions showed basically consistent geographical patterns. Small specimens of Parathemisto, which dominated the material, were usually most abundant in subarctic water of the North Atlantic and in mixed oceanic-neritic water east of the Firth of Forth in the North Sea. Those in the North Sea and along the Atlantic coasts of France and the British Isles belonged to P. gracilipes, which on rare occasions was found also over the American shelf, while others widely distributed in the North Atlantic were mainly P. gaudichaudii, a species seldom collected in the North Sea.

In autumn, but not so much at other times of the year, relative proportions of two forms of Parathemisto gaudichaudii varied between the eastern and western North Atlantic. Whereas form bispinosa was most abundant between Iceland and the west of Britain, compressa predominated from Iceland to Newfoundland.

Numbers were always more by night than by day, the difference being greatest in the summer and in a subarctic region, north-east of Newfoundland, where warm water of the Gulf Stream is likely to have encroached. This diurnal change was mainly effected by larger specimens, though small ones contributed to a lesser, seasonally variable, extent.

Seasonal abundance varied geographically, not only in magnitude, but also in the frequency and timing of peaks. Whereas two or more small maxima occurred in neritic regions and warmer waters of the North Atlantic Drift current, a single large peak was characteristic in subarctic water and cooler parts of the Drift, developing off Newfoundland between winter and late summer, but off Iceland from spring to early autumn. In all regions, decline in abundance was rapid, numbers becoming very low by late autumn. Generally, with increase in numbers, small individuals gradually outnumbered larger ones until they overwhelmingly dominated, most large animals having left the sampled level just prior to peak abundance. Following the autumn decrease, however, smaller specimens were no more numerous than others, being rare except at latitudes of Newfoundland and southward.

Annual fluctuations in abundance were usually small compared to other changes. A general increase from 1962 to 1964 was slight. The only coordinated and significant event occurred in 1964 when hyperiids from east of Scotland and west of the British Isles became noticeably more abundant than in other years. Variations in the relative proportion

of small and large specimens suggest that timing of the seasonal cycle may have fluctuated annually.

B ACKNOWLEDGEMENT

I acknowledge with gratitude the assistance of Mr G.M. Spooner (Plymouth, England) and Prof G. Thorson (Helsingør, Denmark) who aided me with my search through the literature and Dr I. Hallgrimson (Reykjavik, Iceland), Dr E. Smidt and Mr Kr. Vagn Hansen (both of Copenhagen, Denmark), Dr F. Evans (Cullercoats, England), Dr R. Hamond (now Cronulla, Australia), Mr J. Corlett (Lowestoft, England), Dr J.H. Fraser (Aberdeen, Scotland), Dr M.J. Dunbar (Montreal, Canada), Dr T.E. Bowman (Washington, U.S.A.) and Dr E.L. Bousfield (Ottawa, Canada) who helped me obtain specimens with which to supplement those of the CPR collection. Further, Dr J.M. Colebrook (Edinburgh), Mr R.M. Morrison (Glasgow, Scotland) and Dr A.I. Rees (Southampton, England) offered advice on statistical techniques while Mr D.H. Jones (Edinburgh), Dr W. Vader (Espegrend, Norway), Dr J.S. Gray (Robin Hood's Bay, England) and Mr G.M. Spooner provided me with unpublished information.

To all the specialists at the Oceanographic Laboratory in Edinburgh who helped me to recognize and appreciate the variety of plankton in the North Atlantic and North Sea I offer my sincere thanks.

A special due is owed to my supervisor, Mr R.S. Glover (Director of the Oceanographic Laboratory), for his guidance and valuable criticism of the manuscript and to Prof J.E.G. Raymont (Head of the Department of Oceanography at Southampton University), for further encouraging me to

complete the writing.

The work took place at the Oceanographic Laboratory of the Scottish Marine Biological Association and was financed by contract N 62558-3612 between the Association and the Department of the United States Navy, Office of Naval Research.

C INTRODUCTION

C1 Relationships between plankton and water mass

It is generally assumed that, because organisms in the plankton are disseminated mainly through drifting, patterns in their distributions reflect the circulation of water. As pointed out by Fraser (1962), the various distributions of particular plankton species depend on 1) the temperature, chemical content and biological history of the water, 2) the limitations of survival and reproduction imposed on the organism by these properties, and 3) the alteration and shifting about of the water by weather, topography, tide, and Coriolis force, etc.

Though its temperature may be altered according to latitude and season, a water mass may well maintain a characteristic fauna (Bary, 1963), presumably through the influence of certain chemical and biological factors, the nature of which are now only beginning to be understood. Lewis and Ramnarine (1969), for example, have recently found that trace amounts of cobalt and zinc may enhance the growth of the copepod Euchaeta japonica at certain stages in its development. Hutchins (1947) suggests that, at least for inshore organisms, the environmental conditions in which reproduction takes place are more restrictive than those necessary for mere survival of the organism. Thus, although members of a population may be spread over a wide area, it may breed in only a part of that area.

Although populations living in surface waters may be carried into unfavourable environments there is evidence that such organisms might be able to descend into a deeper layer of water where a counter current might return them to more favourable surroundings. Bousfield (1955) found that, in its late naupliar and cypris stages, a barnacle may be taken back to its place of origin at the head of an estuary through descent into the deep saline inflow. Mackintosh (1937) found several species of zooplankton which take advantage of a deep current, running counter to the flow of their Antarctic surface-water environment.[1] Whereas some species which live near the surface during the day spent their nights at depth, others showed little diurnal vertical migration but went below for the winter. Thus, to understand plankton distributions in the surface layers, it is necessary to consider possible vertical migrations of the inhabitants with reference to patterns of water circulation at different depths.

The number of species is usually more in warm than in cold latitudes (Sverdrup et al., 1942 - p 867; Fischer, 1960), but the volume of the smaller zooplankton may on average be less (Foxton, 1956). Whereas cold waters often support a large seasonal maximum in abundance, the warmer regions generally produce relatively small numbers of plankton rather evenly throughout the year (Grice and Hart, 1962). In certain regions of upwelling in tropical waters,

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[1] An alternative mechanism, of horizontal cyclonic circulation, is suggested by Hardy (1967 - p 481).

however, nutrients supplied to the upper layers can encourage a greater abundance than would otherwise occur (Longhurst, 1967).

Soviet investigators, using the Juday net from 1959-1962, have shown the distribution of biomass in the Atlantic (Kanaeva, 1963 - chart) while British surveys with the CPR from 1958-1965 indicate the diversity of surface-water species (and an "index of biomass") for the North Atlantic (Scottish Mar. Biol. Assoc., 1968 - Fig. 1).

Dunbar (1968 and 1969) has suggested that the greater diversity among poikilotherms in tropical waters, as compared to boreal waters, may be the result of a more rapid evolution whereby speciation is now reaching its final stages and nearly all niches are filled. Delayed by a longer generation time, the evolution of organisms in colder water, on the other hand, may still be at an early phase, as evidenced by a high degree of morphological similarity (forms, subspecies, sibling species) and a certain ecological pliability among boreal types.

C2 Circulation of water bodies

In those regions of the North Atlantic surveyed by the CPR, two systems of water movement dominate the near-surface distribution of plankton. One, the subarctic system, is a large counter-clockwise gyre with the Labrador

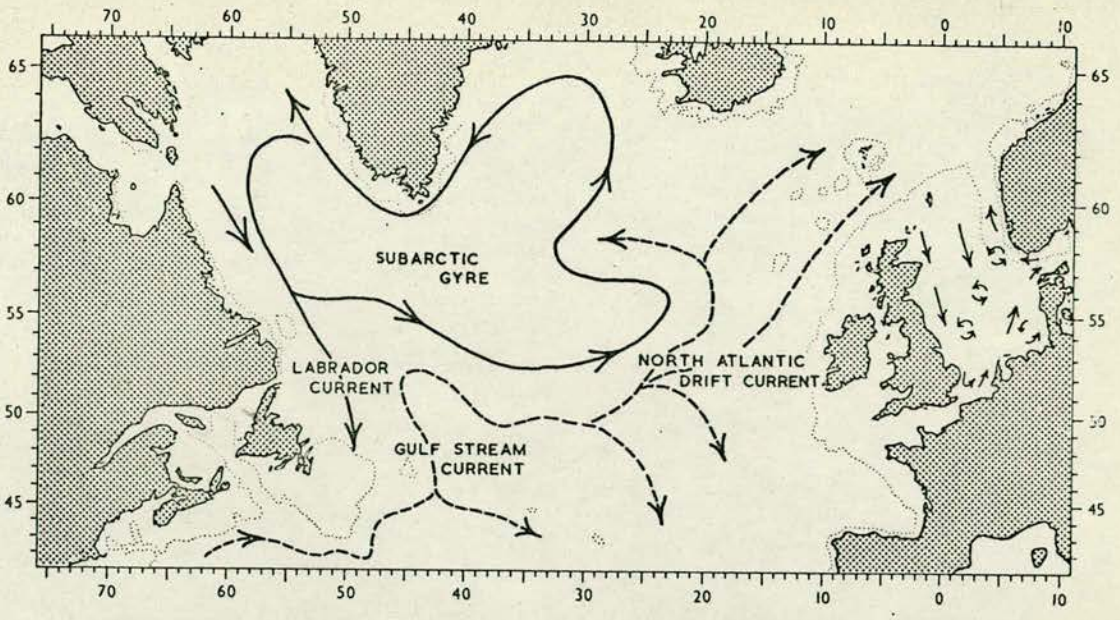

FIGURE 1 -- Generalized diagram of surface circulation for the North Atlantic (from Scottish Mar. Biol. Assoc., 1968) and North Sea (modified from Bohnecke, 1922). In the North Atlantic, the Gulf-Stream system, including the North Atlantic Drift current, is illustrated by pecked arrows and the subarctic system, including the Labrador current, is represented by heavy, solid arrows.

Current on its west side (Sverdrup et al., 1942 - p 682). It includes a branch of the Labrador Current extending to the south (Fig. 1). Whereas subarctic water, from mixing of Arctic and North Atlantic waters, is cold, that originating from the south is comparatively warm.

The warm system begins with the Gulf Stream current flowing eastwards away from the American continental shelf. Beyond the Grand Banks of Newfoundland this current bends northward and makes a loop which appears to follow the contours of the western basin of the North Atlantic (Fig. 1).

Where the Gulf Stream mixes with subarctic water and becomes broadened, meandering, and hydrographically indistinct, it is known as the North Atlantic Drift current and continues the journey branching east and north-east. As indicated by Sverdrup et al. (1942) part of the north-eastward branch of the Drift current turns west and feeds into the Irminger current, contributing Atlantic water to the subarctic system, while other parts continue to flow north-east into the Norwegian Sea and North Sea.

Immediately below the circulation of surface waters in the North Atlantic, flow the intermediate water masses. One of these, the Mediterranean Intermediate Water, branches northward from the Mediterranean Sea and turns westward under the southern (warm) part of the North Atlantic Drift current to proceed south-westwardly across the ocean. Under the Gulf Stream current this water joins other currents of intermediate depth, proceeds north-eastwardly under the North Atlantic Drift, picks up Arctic Intermediate Water and then turns north (Sverdrup et al., 1942 - Fig. 188, p 686). Such undercurrents could alter the distribution of those members of the surface plankton which migrate to great depths. This may be particularly true for organisms sinking from water in the southerly part of the Drift, for they could be carried in Mediterranean Intermediate Water crossing to the American side.

According to Sverdrup et al. (1942) circulation in the northern part of the North Sea is predominantly a

counter-clockwise gyre with southward inflow of North Atlantic Drift water proceeding along the east coast of Scotland and northward outflow from the Baltic extending along the western borders of Sweden and Norway. Böhnecke (1922) indicated that this northern circulation may be separated from waters to the south by a series of broad eddies. Figure 1 (a simplification of Böhnecke's illustrations) shows how the eddies penetrate furthest on the western side.

In the southern part of the North Sea, the influence of Atlantic water is reduced. Künne (1937) showed that at times the presence of this water, identified by indicator species, extends from the north into the Dogger Swirl (off the east of England) and from the west into the Southern Bight (east of Dover Straits). Russel (1939) and Künne (1937) make it clear that those waters remaining in the southern North Sea are basically endemic and, with characteristic plankton, occuppy mainly a region off the coasts of Belgium and the Netherlands. Only seldom is this region penetrated by species indicative of Atlantic admixture (Verwey, 1964 - p 304).

C3 Amphipoda Hyperiidea -- the importance of genus Parathemisto in the North Atlantic and North Sea

Most members of the Order Amphipoda (Class Crustacea) have in common a body which is laterally compressed and without a carapace, eyes which are compound and without

stalks, and antennae, maxillipeds and pereopods which are without exopodites. Characteristically the pereopods take two or more orientations (hence "amphi-poda") and may possess gills and, in the female, oostegites. Pleopods and uropods usually number three pairs each. (See Borradaile et al., 1935, and Barnes, 1963.)

There are four suborders of Amphipoda; two of these, the Hyperiidea and Gammaridea, include the majority of species. Members of the suborder Hyperiidea are typically pelagic and entirely marine, whereas those of Gammaridea are mostly benthonic and, though mainly marine, include some freshwater species. A third suborder, Caprellidea, occupies two specialized niches: the family Caprellidae (skeleton shrimps) feeds on hydroid polyps, bryozoans and other animals of the marine benthos and the family Cyamidae (whale lice) parasitizes the exterior of whales and a few fish. The fourth suborder Ingolfiellidea, discovered in the present century (Hansen, 1903), is found mainly interstitially in marine and freshwater habitats ranging from the depths of Davis Strait in the North Atlantic to the heights of the Pyrénées-Orientales in southern France (Spooner, 1960; Coineau, 1963).

Stephensen (1925) showed that hyperiid genera are few in the northern parts of the eastern North Atlantic; particularly when compared to the diversity of types which occupy warmer water further south. He divides his collection of surface-living hyperiids, from off the Atlantic coast of

Europe, into three latitudinal groups. Most species lived south of 30-40°N and relatively few inhabited waters north of 50°N while between 40 and 50°N species from both zones occurred sparsely. At times, however, those from the intermediate region, including some southern forms, were found to have been carried by a strong current to the north.

In the western North Atlantic this situation is similarly reflected. Grice and Hart (1962) classified the hyperiids collected from surface waters between New York and Bermuda according to four environments: - shelf, slope, Gulf Stream and Sargasso Sea. Out of fifty-five species only eight occurred in the cold surface waters over the continental shelf and, of these, only two were characteristic inhabitants; that is, neither coming from subsurface levels nor resulting from the seasonal intrusion of warmer waters. These two species, which accounted for a numerical abundance of amphipods over the shelf, several times that in the other waters (Grice and Hart, 1962 - Appendix Table 2), belonged to the genus Parathemisto.

Lucas, Marshall and Rees (1942) mentioned the presence of Parathemisto in collections of the Continuous Plankton Recorder from the region of the Faero-Shetland Channel. Marshall (1948) described how the genus is distributed in the southern North Sea and Vane (MS1951), taking a greater area of investigation, was able to expand this knowledge to include the northern North Sea and parts of the eastern North Atlantic.

The genus Parathemisto is without doubt the principle representative of hyperiids in surface waters of these eastern regions of the North Atlantic. Of nine species of Hyperiidea identified by Vane (MS1951) in CPR collections taken from the North Sea and between Iceland and the British Isles, three were found by Stephensen (1925 - p 228-31) to predominate in waters to the south. From the results of Stephensen (1923-5) and Vane (MS1951), eight species might possibly be considered as characteristic of northern waters. These belong to four genera, Typhaena, Hyperia, Hyperoche and Parathemisto, but, according to the quantitative observations of Vane, only Parathemisto spp. were abundant. Bowman (1960), in reviewing the position of Parathemisto in all oceans, considered that this one genus overwhelmingly dominates the abundant amphipod fauna of the colder regions.

C4 Present state of knowledge concerning Parathemisto

The genus Parathemisto has seven known species (Bowman, 1960). Whether these should be separated between two subgenera (Barnard, 1930; Bowman, 1960; Kane, 1966), however, may be disputed (Evans, 1968a). Four of the species occur in the North Atlantic and North Sea (Bowman, 1960). Confusion in nomenclature between these has reduced much of the value of earlier work. As shown by Stephensen (1924), the three species gracilipes, gaudichaudii and abyssorum were at times referred to a single name, oblivia, of a species not adequately described. Parathemisto

gracilipes and P. gaudichaudii are morphologically very similar and, despite the recognition by Barnard (1930) of a definitive character, may sometimes be difficult to separate. Both these species have long-legged (bispinosa) and short-legged (compressa) forms which, because of intermediates (Stephensen, 1924; Mogk, 1927), may occasionally be hard to distinguish.

Parathemisto gaudichaudii and P. gracilipes are known to form massive aggregations and dominate the plankton in localized regions (eg. Gray and McHardy, 1967). Probably because of such swarming, Parathemisto becomes economically available as a food for large predators. For a number of birds, mammals and fish, this genus (as P. gracilipes, P. gaudichaudii, P. abyssorum or P. libellula depending on geography) may form a substantial part of the diet (eg., Ealey and Chittleborough, 1956; Nemoto, 1968; Gray and McHardy, 1967). At least two species of the genus, P. gaudichaudii and P. abyssorum, may suffer from a parasite of the nervous system, Thalassomyces marsupii (Kane, 1964; Vader and Kane, 1968).

Although Parathemisto may ingest detritus and phytoplankton (Dunbar, 1946; Siegfried, 1965), it is primarily a carnivore, feeding mainly on copepods and, to a lesser extent, on euphausiids. Among the larger zooplankton, including young fish, it may be, not only an important competitor for food, but also a dangerous predator (Hardy and Gunther, 1935; Williamson, 1950).

Work on various species of Parathemisto has suggested that, depending on the species, seasonal breeding may occur over an extended period, a single female reproducing for one, two or even three seasons during a life time of one or two years; each time she might release, successively, one, two or three broods (Bowman, 1960; Kane, 1963; Evans, 1968b). Whereas P. abyssorum and P. libellula appear to breed only once after taking two years to mature (Bogorov, 1940; Dunbar, 1957), it is possible for P. gracilipes to reproduce during two seasons after first reaching maturity in only a few months (Evans, 1968b).

Adults of Parathemisto gracilipes which spawn in late summer may again breed in the following spring, after having passed the winter in a state of immaturity (Evans, 1968b). It is possible that P. gaudichaudii also may revert to the immature condition between breeding periods (Siegfried, 1965; Kane, 1966).

Although reproduction in Parathemisto gaudichaudii may be spread over a greater part of the year, there are one or perhaps two periods of peak activity, the timing of which seems to vary with the region (c f., Stephensen, 1924; Bigelow, 1926; Vane, MS1951; Siegfried, 1965; Kane, 1966). The nature of these geographical variations is not clear, however, though in one case temperature was suggested to have been a controlling factor (Stephensen, 1925).

All species of Parathemisto are found in the cooler regions of the world oceans, where they live predominantly near the surface (Bowman, 1960). In the North Atlantic, P. libellula and P. abyssorum occur in waters of mainly Arctic origin (Ekman, 1953; Dunbar, 1964) whereas P. gaudichaudii would appear to prefer those regions which are chiefly subarctic; this is suggested by a comparison of the distribution of water masses (Sverdrup et al., 1942) with the occurrences of this species in the North Atlantic (Stephensen, 1923 and 1924). Of these oceanic species, P. abyssorum is known to frequent deeper waters (eg. below 300 m) more often than the others (Stephensen, 1925). Parathemisto gracilipes, on the other hand, though it may exceptionally be found below 300 m, is primarily a neritic species living in near-surface waters over the continental shelf. (Stephensen, 1924). Where warmer waters prevail, this species appears to survive better than P. gaudichaudii (Bary, 1959; also c.f. Fig. 1 and Stephensen, 1924). The young of P. gaudichaudii, at least those in the Gulf of Maine, are found on average to find a shallower position in the water column, than the adults (Bigelow, 1926).

The area of the North Atlantic and North Sea sampled by the present survey of the CPR is generally outside waters inhabited by P. abyssorum and P. libellula, but extends over most of the regions occupied by P. gracilipes and P. gaudichaudii.

Published information on the distribution of Parathemisto gracilipes lacks information about its

abundance in the northern North Sea and in the western North Atlantic. Vane (MS1951), in his MSc thesis, emphasized the importance of the central region of the North Sea as a major breeding place for the species, but generally his work is not known (it was not mentioned, for example, by Evans, 1968b, who commented on the insufficiency of data pertaining to this species in the North Sea). Until the work of Grice and Hart (1962), the existence of P. gracilipes near the American coast was not recognized (Bowman, 1960); as yet its relative importance there is not understood.

In the North Sea and vicinity, Parathemisto gracilipes is known as an indicator of mixed neritic and oceanic water (Russel, 1939; Fraser, 1961; Southward, 1961-3). Bowman (1960) had suggested, from apparent absence of this species off the American coast, that there was insufficient water of the appropriate character to support its existence.

Although the geographical range of Parathemisto gaudichaudii in the North Atlantic is fairly well known (Bowman, 1960; Dunbar, 1964), its relative abundance in different areas is only roughly quantified. Generally its numbers are great in regions where subarctic water (as defined by Sverdrup et al., 1942) is known to circulate (Fig. 1), but few in waters of the Arctic and North Sea (Stephensen, 1923 and 1924). Also animals may be scarce over shoal areas, such as Georges Bank, where surrounding deep waters are rich in the species (Whiteley, 1948). A seasonal shift in abundance may take place, along the

American shelf at least, whereby the distribution extends northward with summer warming and retracts as autumn commences Bigelow and Sears (1939).

Even though bispinosa and compressa forms often appear together their relative numbers may differ depending on the region (c f. Stephensen, 1923 and 1924; Bigelow, 1917 and 1926; Barnard, 1932; Bousfield, 1951; Kane, 1966 and Shen, MS1966), the time of year (Bigelow, 1917 and 1926; Kielhorn, 1952; Vane, MS1951), and the depth (Bigelow, 1917; Stephensen, 1924).

C5 Objectives of this study

The collections of the Continuous Plankton Recorder (CPR) provide a uniquely broad coverage of plankton in the near-surface waters of the North Atlantic Ocean and North Sea. I was given the opportunity not only to assist for a period of three years in analysis of the wide spectrum of organisms available in these collections, but also to examine the distribution of those belonging to a particular taxonomic group.

For one such group, the hyperiid amphipods, the data seemed particularly suitable for investigation. The size range represented is that especially well sampled by the CPR and the abundance is sufficiently great to allow for a quantitative assessment of variations.

After the importance of Parathemisto was recognized, it became necessary to modify the initial objectives of the project. As a greater understanding of variations in the abundance of hyperiids could be obtained by concentrating on this genus -- its species, forms, size composition and maturity stages -- less emphasis than originally intended was placed on the taxonomic study of rare genera. The aims of the present study, therefore, are to recognize variations in abundance, to characterize geographical and temporal differences in numbers and, where possible, to relate these to changes in the population and its environment.

Thus, I am going to show that consistent geographical patterns of distribution were revealed which can be clearly associated with the circulation of surface waters. Two species are shown to be predominant, each exclusively abundant in separate water masses. Two forms of one of these species, Parathemisto gaudichaudii, are widely dispersed over the North Atlantic but showed distinct geographical differences with respect to their relative numbers.

Numbers, which were always more by night than by day, changed throughout the year according to the reproductive cycle. The magnitude, frequency and timing of seasonal increases varied geographically, probably in relation to environmental restrictions on breeding. Though abundance changed little from year to year, there is some evidence suggesting that timing of the reproductive cycle might fluctuate annually.

This investigation is designed to provide descriptive information as a background for further work. Evidence is not collected with a view to testing hypotheses. Rather much of its value is in providing a basis for the formulation of problems yet to be examined.

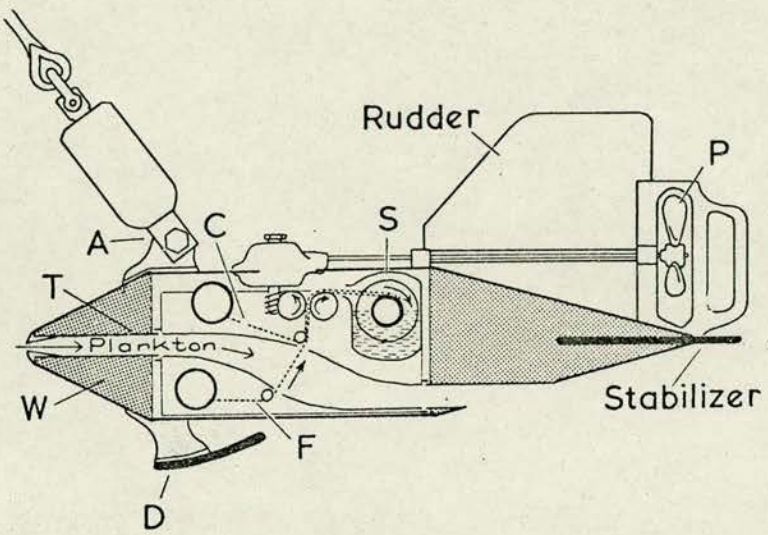

FIGURE 2 -- The Continuous Plankton Recorder, a schematic cutaway drawing (modified from Glover, 1967) to illustrate functional relationships between the tunnel (T), filtering silk (F), covering silk (C), storage chamber (S), towing attachment (A), propeller (P), weighted front (W) and diving plane (D).

D THE CONTINUOUS PLANKTON RECORDER

Professor A.C. (now Sir Alister) Hardy designed the CPR in order to overcome some of the problems of examining plankton variability. For broad surveys conventional nets may provide discrete samples at isolated locations, but often give widely dissimilar results due to the patchiness of plankton distribution. By collecting a continuous sample over a long distance the CPR not only supplemnts these other observations with connecting information, but also eliminates the often troublesome variability related to the aggregation of plankton.

The CPR is a robust and reliable plankton sampler that can be towed from large vessels in oceanic conditions, without the aid of trained personnel. Its original design and further modifications are described by Hardy (1936 and 1939).

Briefly the CPR functions as follows (see Fig. 2). Water entering the sampling aperture passes through a tunnel (T) and plankton is strained off onto a continuously moving band of silk (the filtering silk, F). A second band of silk (the covering silk,C) then covers the filtered plankton, holding it in place while both bands wind onto a roller within a storage chamber (S), where formalin fixes and preserves the sample. The bands of silk are driven by rollers mechanically linked to a propeller (P) powered by its movement through the water.

D1 Some general features of plankton sampling

Plankton samplers seldom, if ever, provide completely representative samples. Those designed to collect one type of organism usually exclude some others. No single sampling method is capable of representing the abundance of all the various organisms comprising the plankton. A device may be chosen according to its capacity 1) to receive samples which are sufficiently large or numerous, 2) to accept and retain specimens of an adequate range of size and 3) to capture organisms capable of active escape. However, any selection within the range of one of these three variables will inevitably affect the scope of the other two.

The purpose of the CPR is to obtain a representative sample of the plankton in general and some compromise is made to collect a range of organisms.

Whereas smaller organisms are often well represented in a small volume of water, larger ones may be relatively scarce. Although it might be preferable to sample a larger volume and better represent those less numerous specimens of greater size, the more abundant small plankton would soon plug a fine or medium mesh and prevent further capture.

Some species known to swarm may generally appear absent or rare though they occasionally turn up in large numbers. These organisms would be better represented by numerous small volumes broadly covering time and space rather than in fewer large ones of limited extent.

A small size of sample was chosen for the CPR not only to reduce clogging but also to make the numbers collected more manageable to count. In every ten miles covered by the sampler plankton is filtered from only three cubic metres of water. Nevertheless, because each 3-m^3 sample is taken over such a distance, it can be regarded as equivalent to an accumulation of numerous smaller samples. The CPR sample would hence represent an average composition and density, unaffected by variability due to plankton aggregations.

The pore-size of a filtering mesh determines the size of organism retained. Whereas a fine mesh would strain off the smaller plankton but become clogged long before the less numerous larger specimens had been adequately sampled, a coarse net would allow a large volume of water to be screened for bigger individuals but fail to hold back the smaller ones.

The filtering silk of the CPR is of medium-size mesh (pore space of 0.2-0.3 mm square) and consequently can retain few organisms with dimensions less than 0.3 mm. Also the sampling aperture is small (12.7 mm square) and is therefore likely to accept only a portion of that plankton which is larger. Furthermore, the sizes sampled may depend on the shape and orientation of specimens and the amount of clogging of meshes.

The length of the most common hyperiid in the present survey, Parathemisto gaudichaudii, has been shown to

vary, in the Southern Ocean, from 2.2 mm for the smallest post-broodpouch animals to 33 mm among the largest adults (Kane, 1963). The medium mesh used in the CPR is likely to retain all of the younger stages (except perhaps those that approach with the long axis perpendicular to the plane of the filter) but the small sampling aperture may exclude a portion of the very large ones. In the present study, specimens longer than 15 mm were usually found to be damaged.

Actively swimming organisms of the plankton avoid capture with variable degrees of success. Older euphausiids have been shown to escape collection more readily than juveniles (Marr, 1962) and larger larval fish are taken less frequently than smaller ones (Colton, Honey and Temple, 1961; Colton and Marak, 1962). Colton et al. (1961 and 1962) have demonstrated that high speed samplers, including the CPR, obtain a larger proportion of the older larval fish than do conventional nets.

This successful sampling is probably due to not only the speed of operation but also, the unobstructed approach to the sampling aperture. Whereas slow speed nets have bridles and other obstructions in front, relatively undisturbed water precedes the CPR and other samplers successful at collecting actively swimming plankton, for example, the "Gulf III" (Gehringer, 1952) and the "Catcher" (Bary et al., 1958).

Soft bodied organisms are particularly susceptible to damage by high speed samplers. Much of the injury can be reduced, however, by decreasing pressure of water entering the sampler through gradual increase in the volume of the sampling passage. Clarke (1964) has made particular use of this technique in devising his "Jet Net" which, at high speed, causes less damage to plankton than does either the Gulf III or the Catcher.

The CPR is also designed to reduce pressure and decrease damage to organisms. The cross-sectional area of the tunnel at the filtering silk is about 32 times that at the aperture. This is about ten times the ratio (3.6:1) considered adequate for the Gulf III (Gehringer, 1962). Even so, damage by the CPR can make delicate animals, such as medusae, very difficult to identify. As demonstrated by the work of Hunt (1968) on salps and doliolids, however, their recognition is not impossible.

D2 Special features of the CPR

Whereas some samplers collect single samples and others take several discrete ones (eg., Motoda, 1962; Fish and Snodgrass, 1962; Williamson, 1963; Longhurst et al., 1966), the CPR gathers a continuous record of plankton, rather resembling a series of small overlapping samples. This record is generally subdivided into segments and the

material from each can be examined, stored, and reexamined without its removal from the silk upon which it was originally collected. This treatment eliminates the problems of handling which often occur with collections taken by other means.

Small variations in the plankton tend to be smoothed out by the continuous method of sampling. Since the samples then resemble averages, large-scale variations can be distinguished more readily from variations related to plankton patchiness.

A certain amount of flattening of specimens is caused by the mechanism for continuous sampling. Generally it is not serious and, for some species, may even assist in identification by exposing diagnostic features.

In hyperiids, the body and most appendages are generally compressed laterally and, in this plane, withstand flattening exceptionally well. The uropods are normally dorso-ventrally oriented, however, and sometimes become damaged by flattening along their medial and lateral margins. Moreover, the third of these appendages possesses, along the inner margin of its endopodite, the most important character for separating the two common species of the present material. This feature is often obscured, especially in smaller specimens.

The CPR is the only plankton sampling device available that has been shown to remain stable and hold a constant depth while being towed at cruising speeds within the 12 to 17 knot range for most ocean-going vessels. This

capability makes the instrument available for operation from ordinary merchant ships, weather ships and other vessels engaged in routine passages across the ocean. Furthermore the CPR can be launched and hauled by the normal crew members of such vessels without supervision or training from scientific personnel. Because of its capacity for unattended continuous sampling at cruising speed, the CPR became the instrument behind an idea for a broad geographical survey which could be repeated at regular intervals (Hardy, 1936). Promotion of this idea has resulted in an increased number of ships towing CPR samplers monthly over a widening area (for a recent report of progress see Glover, 1967).

D3 The CPR survey

Since its inception in 1932, the CPR survey has expanded geographically from an initial coverage of the southern North Sea to one spreading over most of the North Atlantic. Except for interruption between 1939 and 1946, the temporal interval of sampling has remained monthly.

Since 1958, the survey has progressively extended westwards to the coast of North America. For the years 1962-5 the coverage is considered sufficiently complete to form a basis for studying the distribution of hyperiid amphipods over the North Atlantic Ocean. During this period the only major gap was in the centre of the southern

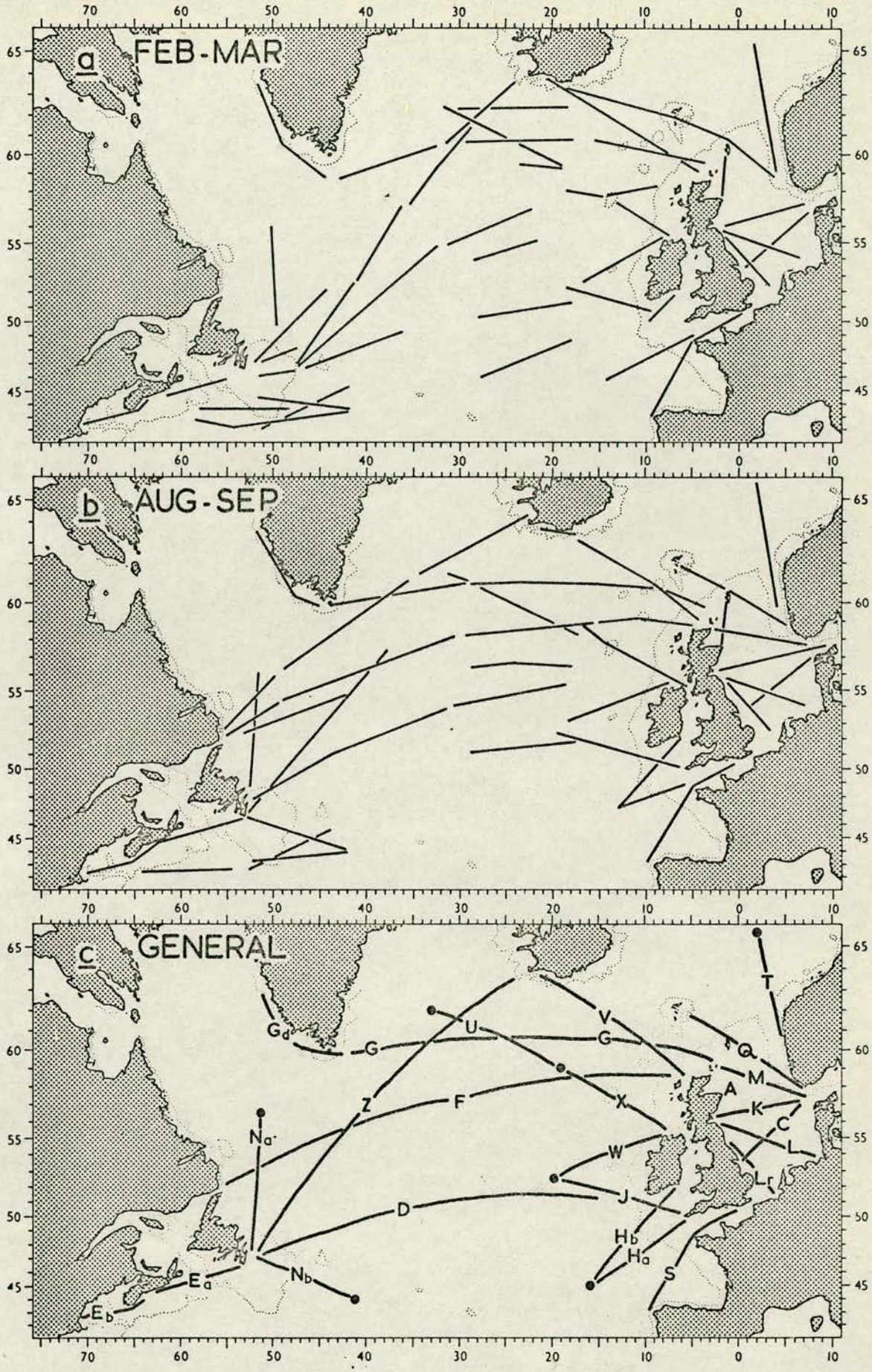

FIGURE 3 -- Legend at foot of page following.

boundary of the survey area. Other gaps still occur between the established shipping routes and constitute a deficiency inherent in the use of merchant and weather ship facilities. Even so the coverage is far more complete than could ever be achieved by vessels presently available for research.

The course of a few routes may shift southwardly in winter as the ships avoid floating ice. The average positions for February-March (Fig. 3a) and August-September (Fig. 3b) in the years 1962-5 indicate the extent to which these seasonal alterations might occur. Where they are significant (eg. north of Newfoundland), seasonal comparisons should be considered with caution.

Routes whose courses are well established and regularly sampled are referred to by code names (Fig. 3c). When relatively detailed geographical presentation is justified, results are assigned to "statistical squares", areas of usually 1° latitude by 2° longitude. Those statistical squares sampled in August and September, 1962-5, are illustrated in Fig. 4a. When a more generalized expression of distribution is required, the data are referred to larger areas, the "standard areas". These regions, shown in Fig. 5a, are designed to facilitate comparison with

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FIGURE 3 -- Routes sampled by the Continuous Plankton Recorder: a, in February and March, 1962-5; b, in August and September, 1962-5; c, in general. All routes have codes (letters); some are paths to and from weather stations (•).

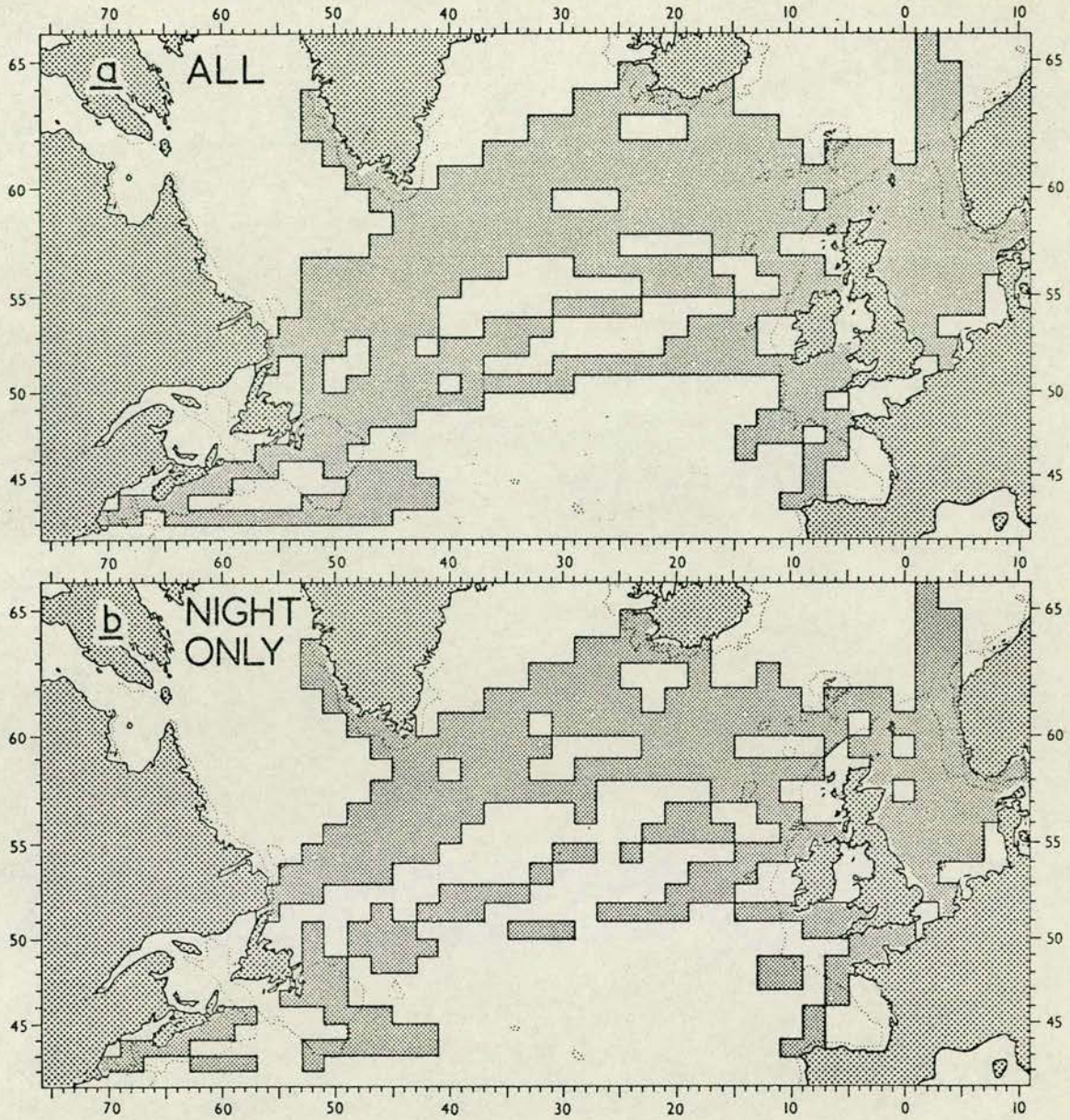

FIGURE 4 -- Statistical squares sampled in August and September, 1962-5: a, through all times of day (ALL); b, by night only (NIGHT).

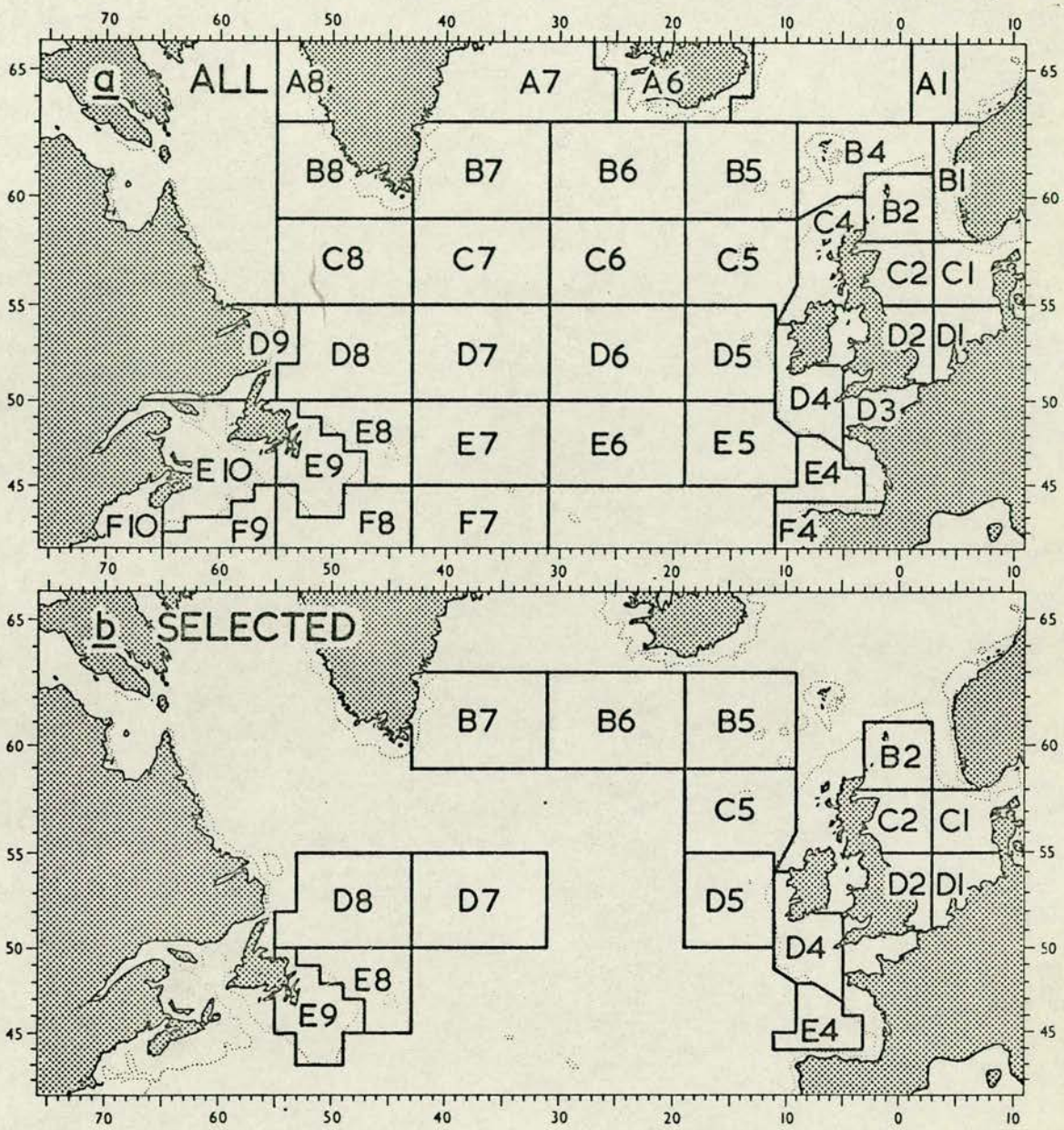

FIGURE 5 -- Standard areas (with their code letters and numbers: a, sampled to various degrees during 1962-5 (ALL); b, sampled consistently and considered suitable for comparison of the density of hyperiids (SELECTED).

hydrographical data and fisheries statistics (Glover, 1962).

Exploration of the vertical distribution of plankton has been sacrificed in the survey in order to obtain an extensive geographical and temporal coverage (eg. Fig. 4a). Only the depth of 10 m is sampled by the CPR, which is maintained at this level through a fixed arrangement of its weighted front and diving planes (W and D, respectively, Fig. 2) and an adjustment of the length of its towing cable varied according to the cruising speed of each ship.

Diurnal changes in vertical distribution have been recognized in a number of marine planktonic animals. Such is probably reflected in the daylight decrease of hyperiids in the CPR samples. Consequently it is necessary to avoid mixing data from different times of day, especially when other variations in abundance are being considered. Often in the present study, night collections alone were examined, even though this reduced sampling coverage both geographically (cf. Fig. 4, a and b) and seasonally. Mainly due to increased night-length in winter, more statistical squares were sampled at night during this season than in summer (Fig. 6b); compared to this, the annual difference in sampling was small (Fig. 6a).

Seasonal vertical migrations may also account for some of the changes in abundance in surface waters. Sometimes these can be distinguished from variations related to population events through analysis of the size composition.

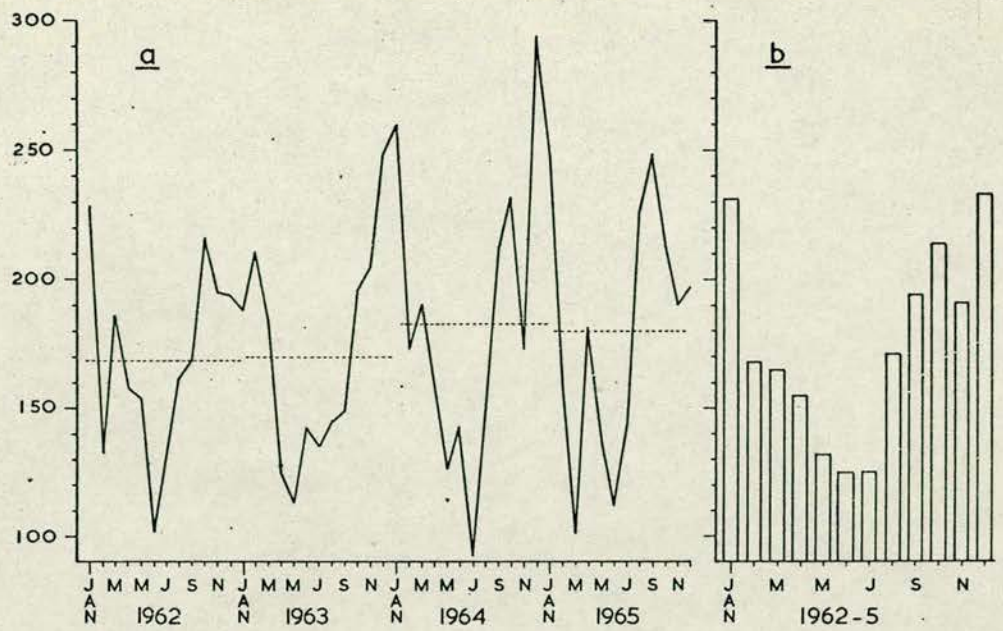

FIGURE 6 -- Number of statistical squares sampled at night during 1962-5: a, means for years (dashed horizontal line) with constituent monthly numbers (solid line) and b, means for months (columns).

Large specimens not preceded by a succession progressively increasing in size, are more likely to have migrated from another depth than to have grown up within the sampled level. Smaller ones succeeding large adults, on the other hand, would probably be a consequence of breeding. The disappearance of specimens from the surface with a reappearance later at a larger size would suggest emigration followed, after a period of growth, by immigration. If, on the other hand, specimens should fail to reappear, their fate might remain unknown, although mortality is an obvious possibility.

The sampling method used in the present work precludes the possibility of detecting either geographical or annual

variations in vertical distribution. Should such variations exist (and there is at present no evidence for them) different interpretations of the results would be possible.

D4 Survey procedures

The double band of silk, with its record of plankton within, is cut into sections each corresponding to a particular 10 miles of towing along the route followed by the ship. The times of sunrise and sunset (determined from a nautical almonac) are used to assign the samples to "night" and "day". Each sample is then treated as a discrete unit and becomes a basis for numerical expression of the densities of taxa counted.

Generally every second sample is analysed. Hardy (1939) found this to be adequate for coastal waters though, in some years when the number of analysts were insufficient to cope in the usual manner with the amount of material being collected, every third sample gave useable results for open-ocean waters. Samples are distributed to analysts by random choice (with the exception that adjacent samples for examination are not given to the same person).

For analysis of each sample the filtering and covering silks are separated and laid, with the plankton facing upwards, on a large moveable transparent glass microscope stage. The organisms are then identified and counted on the silk by three methods:

1. Phytoplankton and other very small organisms are estimated according to their occurrences on the filtering silk, in 20 fields of high power under the compound microscope (1/1400 th subsample).

2. Zooplankton too small to be readily recognizable by eye, are examined and counted through the low-power magnification on step-wise sweeps along diagonals of both filtering and covering silks (approximately 1/40th subsample). See Rae (1952) and Colebrook (1960) for details.

3. Zooplankton in which at least adults are sufficiently large to be recognized by eye, are counted in the whole sample (not a subsample) with the occasional use of a microscope, when required. Attention is paid to specimens as large or larger than the fifth copepodite stage of the common copepod Metridia lucens though young of adults which reach this size may also be counted.

If very small and too scarce to be observed by the first two methods, these young may be overlooked, especially where a high density of other forms could obscure them. For counts of Hyperiidea, which are made exclusively by eye, this problem may not be serious, for a distinctive orange-brown pigmentation obvious in preserved specimens (at least in Parathemisto, Hyperia and Hyperoche) usually attracts attention.

Estimates are expressed as categories to avoid unnecessarily tedious and wasteful counting. A count, judged to lie within the limits of a category, is thus represented

TABLE 1 -- Categories for enumeration of specimens in samples taken by the Continuous Plankton Recorder.

Category number	Number of specimens	Accepted value	Log value[1] x 10
1	1	1	3
2	2	2	5
3	3	3	6
4	4-11	6	9
5	12-25	17	13
6	26-50	35	16
7	51-125	75	19

by an approximate modal point, the "accepted value" (Table 1). Next accepted values are transformed logarithmically: each "log value" = $\log_{10}$("accepted value" + 1) and finally the subsequent "log values", multiplied by ten to remove the decimal, are used in further calculations. It has been shown that transformation to the logarithmic value improves the estimates for subsequent statistical treatment by reducing: 1) the inaccuracy introduced by the use of categories, 2) the size of the standard deviation, 3) the dependence of the standard deviation on the mean, and 4) the bias that occasional large estimates can have on the mean (Colebrook, 1960).

By the routine analysis, hyperiid amphipods are counted separately from other suborders of Amphipoda, but are not classified into genera and species.

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[1]Log value = $\log_{10}(x + 1)$, where x is the accepted value.

D5 Geographical patterns in the plankton

Marine biogeography is primarily based on the plotting of occurrences of species. Earlier information was gathered mostly from easily accessible regions near to shore. Beginning with collections initiated by such expeditions as the British CHALLENGER, the German METEOR, the Danish INGOLF and THOR, etc., the nature of oceanic distributions gradually became realized. As the data collected during these early ventures were from samples widely scattered in space and time, estimates of seasonal or geographical variations were generally unreliable. Furthermore, samples, if quantitative, were not always taken with comparable gear, operated by similar methods. Multiple vessel surveys, such as those made possible by international cooperation (eg., the Norwestlant survey of I.C.N.A.F. and the Indian Ocean Expedition) partly alleviate these difficulties but they are nearly always of limited duration.

The majority of species in the plankton can be associated with one or another water mass. Ekman (1953) defined faunal regions in a very general way. He emphasized that endemic populations of families and genera were of far greater historical importance than endemic populations of species. Now that systematics and biogeography is better known, more can be gained from studying the distributions of species or even subspecific populations. Some of the organisms regarded by Ekman as cosmopolitan (eg., Calanus

finmarchicus, Sagitta gazellae) are now recognized to consist of a number of species and forms, each having its distinct distribution.

The difficulty of identifying young stages may well result in information referring only to adults, the dissemination of which is often wider than reproductive requirements allow (as shown by Einarsson, 1945, for euphausiids and by Hutchins, 1947, for coastal organisms). Ekman (1953) has indicated that expatriate members of a population, carried by water currents beyond the normal breeding area, may give a false picture of the ecological requirements of the species. Despite recognition of this problem, it is still difficult to obtain sufficient data to define distributions on the basis of the self-sustaining population.

Kramp (1959), for example, recognized that planktonic distribution depends not only on currents but also on the differing environmental requirements of various stages in the life history of the animal. Nevertheless, he was forced to describe occurrences of North Atlantic hydromedusae only in the most general terms. Dunbar (1964), similarly, recognized the importance of considering reproduction and relative abundance but was limited by existing data to the mapping of occurrences and expressing only tentative boundaries for the distributions of certain Arctic and North Atlantic euphausiids and pelagic amphipods. Alvariño (1965), though writing of the breeding and abundance of chaetognaths, charted world distributions for the better known species merely as zones.

Einarsson (1945), on the other hand, has been able to use biological data on Euphausiacea in the North Atlantic to full advantage. Not only did he contrast the broad regions over which adolescent and adult animals are dispersed with the more restricted areas of breeding and early growth, but also he incorporated this information (and a knowledge of the vertical distribution) into his maps. Furthermore, Einarsson has noted some interesting regional differences, both in the seasonal timing of reproduction and in the duration of sexual maturation.

Distributions of plankton are often described in terms of water masses. Although this relationship is undoubtedly well founded as a general principle, physical data to confirm identification of the water is often lacking. As the locations of boundaries between water bodies are not fixed and as the numbers and names of water types are variously defined and sometimes in dispute, the exact association between fauna and environment may be poorly understood. Bary (eg. 1963) by introducing the temperature-salinity-plankton diagram has suggested a way by which the plankton can be identified concurrently with the water mass, providing a T-S-P relationship.

It is recognized that the distribution of organisms may change seasonally. The relationship of such fluctuation to expatriation and breeding, needs to be better understood. Chen and Bé (1964) found that, in the western North Atlantic, species of euthecosomatous pteropods present in "transitional"

subarctic water in colder months, were replaced by subtropical types in the warmer season. Similarly planktonic foraminifera occurring in the subtropical North Atlantic in winter were substituted for a quite different, typically tropical fauna in summer (Bé and Hamlin, 1967).

The Continuous Plankton Recorder survey of the North Atlantic and North Sea is limited to collection at one depth (10 m) but has important advantages over other studies of biogeography. While covering a broad geographical region, monthly and over an ever-extending period of years, a consistency of comparable sampling has been maintained. It has therefore been possible to describe basic patterns of the distribution of abundance, not only in terms of geography but also with respect to seasonal and long-term variations (see Colebrook, Glover and Robinson, 1961, et seq.).

An Atlas of the distribution of plankton, in preparation at the Edinburgh Laboratory, will show geographical distributions of some 200 taxa. Partly as a consequence of my contribution to the analysis of plankton, preliminary charts (representing distributions for 1958-1965) are now available. The boundaries thus indicated, it must be remembered, represent distributions in near-surface water. Consequently, horizontal extensions of occurrence below this stratum (such as shown by Einarsson (1945) for the euphausiid Thysanoessa longicaudata in submerged water of subarctic origin) are not detectable by the present techniques of the CPR survey. It is nevertheless rewarding to observe that

most distributions form sensible shapes related, in one way or another, to known patterns of water movement.

The works of Colebrook, Glover and Robinson (1961), Fraser (1962), Shen (MS1966) and Hunt (1968) have enabled me to classify the majority of taxa present in the preliminary Atlas according to the water types with which they appear most closely associated. To these have been added the two hyperiid species whose distributions were determined in the present investigation. The resultant groupings in Table 2 must be considered tentative, principally because information comparable to that for the charts is not yet available on vertical distribution, seasonal change and breeding area.

TABLE 2 -- Plankton organisms distinguished regularly in the CPR survey, classified according to their main surface-water affinities in the North Atlantic (with guidance from Colebrook, Glover and Robinson, 1961; Fraser, 1962; Shen, MS1966; and Hunt, 1968, and the preliminary (unpublished) Atlas of the plankton for the years 1958-65).

Part a

ARCTIC-SUBARCTIC[1] WATER

Diatoms
- Navicula planamembranacea

Dinoflagellates
- Ceratium arcticum

Copepods
- Calanus finmarchicus glacialis
- C. hyperboreus
- Metridia longa

[1]The term "Arctic-subarctic" after Shen, MS1968).

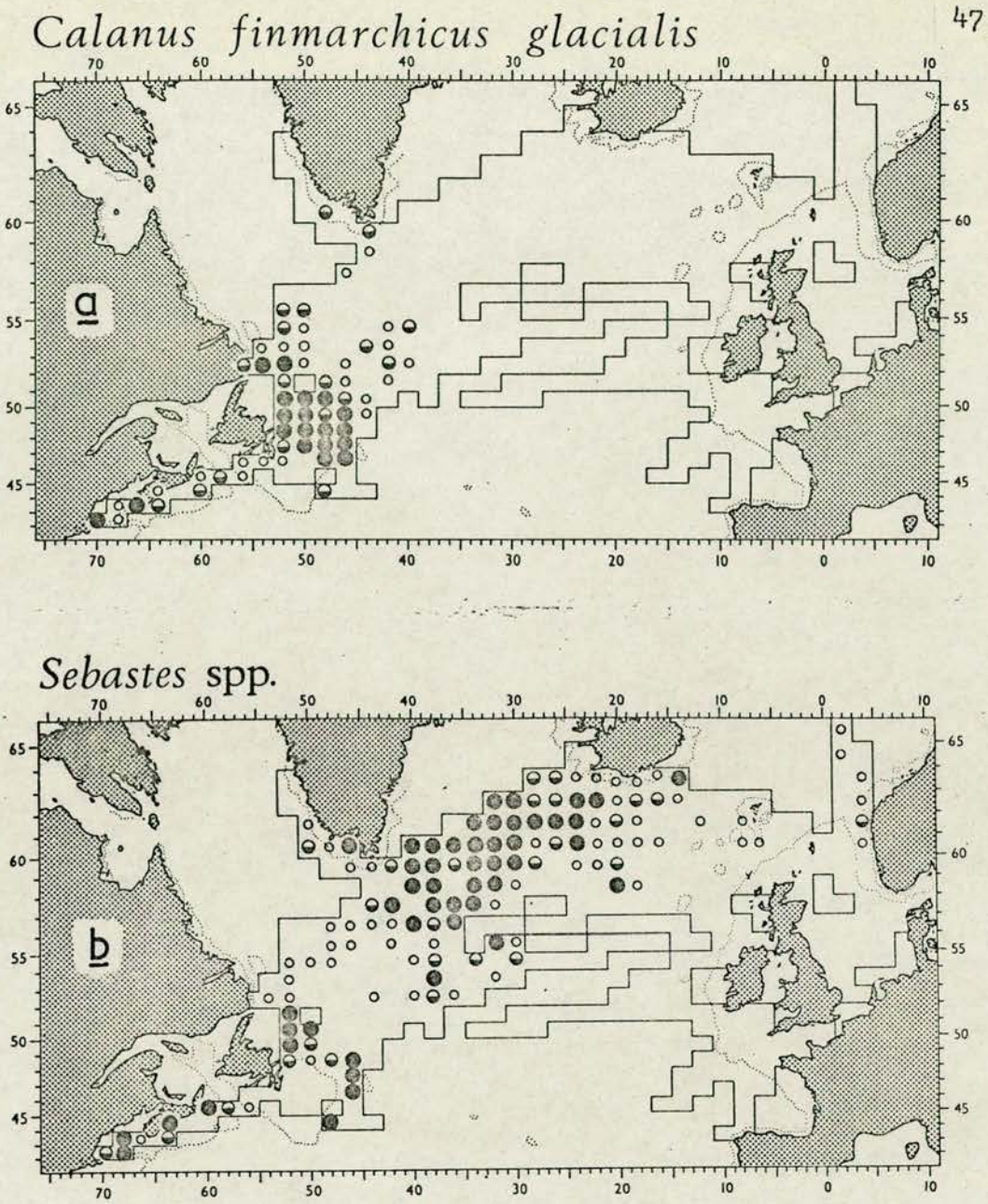

FIGURE 7 -- Preliminary charts from the Atlas of Plankton in preparation at the Oceanographic Laboratory, Edinburgh, showing distributions in surface waters during 1958-65: a, adults of the copepod Calanus finmarchicus glacialis and b, larvae of the fish Sebastes. Open, half-closed and closed circles indicate rare, common and abundant densities, respectively. Region outlined includes only those statistical squares sampled frequently.

Within each grouping there were all grades of distribution. This is indicated by the sequence of geographical distribution given by Colebrook, Glover and Robinson (1961). Moreover some taxa appeared to be common in more than one water body. Wherever possible, therefore, the water type assigned is that which is known to occupy the region where the organism appears in greatest abundance.

It may be recalled, from the introduction, how surface water in the North Atlantic Ocean moves according to two major systems: the cold subarctic assemblage in the north and the warmer Gulf-Stream one to the south. As shown in Fig. 1, these systems meet south of the Grand Banks of Newfoundland to follow an irregular path as North Atlantic water drifting towards the north-east. With this pattern of circulation in mind, therefore, some examples of plankton geography may be examined.

Figure 7 shows the distribution of copepodites V and VI of Calanus finmarchicus glacialis, a copepod which inhabits Arctic-subarctic water of the Labrador Current. Comparison with Fig. 1 indicates that the species is abundant not only off Newfoundland where the Current contributes to the subarctic gyre but also along the coasts of Nova Scotia, New Brunswick and Maine, where it branches south-westward. Typical of the low diversity found in high latitudes (Fischer, 1960), the number of species in this Arctic-subarctic habitat is small (Table 2; **contrast Part a with Parts b,c,d,e, f and g).**

Larvae of the redfish Sebastes, though occurring in the same region of the western North Atlantic as Calanus finmarchicus glacialis, are also particularly numerous south-west of Iceland (Fig. 7b) where C. f. glacialis is not found. This distribution of Sebastes is relatively restricted to subarctic water, particularly in comparison to the extensive occurrence of C. finmarchicus finmarchicus shown in Fig. 8a. Though numerous east of Labrador and Newfoundland, copepodites V and VI of this copepod are widely dispersed from subarctic waters into northern regions of the North Atlantic Drift current and North Sea. Part b of Table 2 names these and the several other species which are characteristically distributed in subarctic water.

At this point it may be well to present the picture for the Hyperiidea which, as illustrated in Fig. 8b, is very similar to that for Calanus finmarchicus finmarchicus (Fig. 8a) and, incidentally, quite like that for the

TABLE 2 -- Part b.

SUBARCTIC WATER

Diatoms
- Thalassiothrix longissima

Copepods
- Calanus finmarchicus finmarchicus
- Euchaeta norvegica
- Heterorhabdus norvegicus

Euphausiids
- total (mainly Thysanoessa longicaudata)

Hyperiids
- Parathemisto gaudichaudii

Fishes
- Sebastes spp.

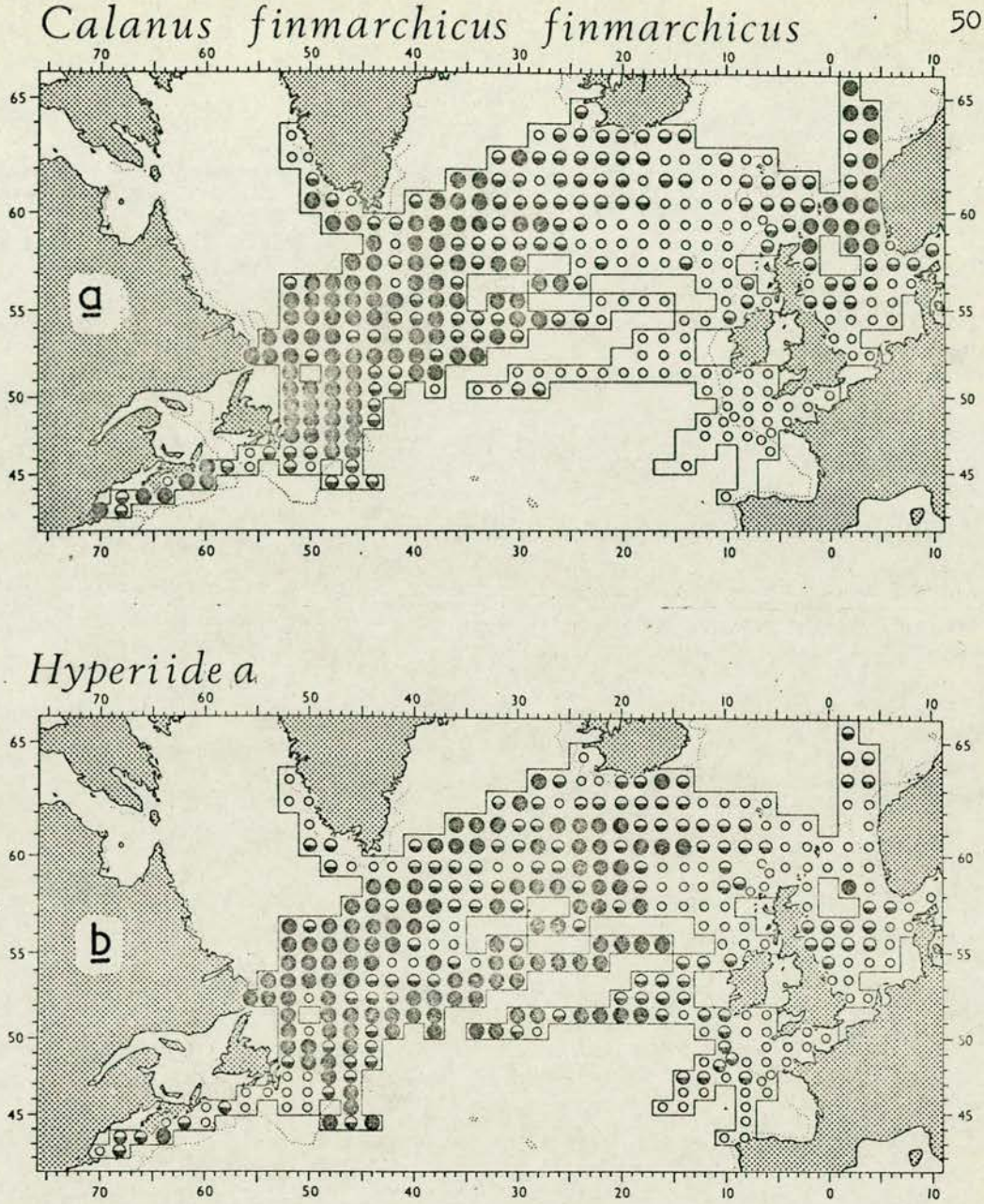

FIGURE 8 -- Preliminary charts from the Atlas of Plankton in preparation at the Oceanographic Laboratory, Edinburgh, showing distributions in surface waters during 1958-65: a, adults of the copepod Calanus finmarchicus finmarchicus and b, Hyperiidea of all species and stages of development. Open, half-closed and closed circles indicate rare, common and abundant densities, respectively. Region outlined includes only those statistical squares sampled frequently.

Euphausiacea. The results of the present survey will indicate, as shown in Fig. 28 (also Fig. 24 et seq.), that two species of hyperiids predominate: Parathemisto gaudichaudii, widely distributed in and beyond subarctic water (especially between Newfoundland and Iceland), and P. gracilipes in mixed water of neritic and North Atlantic Drift origins (particularly in the northern North Sea). These are important findings needed in order to show how the abundance and distribution of hyperiids may be related to other factors in the pelagic ecosystem.

TABLE 2 -- Part c.

OCEANIC NORTH ATLANTIC DRIFT WATER

Diatoms

- Rhizosolenia acuminata
- R. alata var. inermis
- R. imbricata var. shrubsolei
- R. alata var. indica
- R. bergonii
- R. curvirostris
- Dactyliosolen antarcticus
- D. mediterraneus
- Nitschia delicatisima

Dinoflagellates

- Ceratium azoricum
- C. carriense
- C. lineatum
- C. minutum

Blue-green algae

- Trichodesmium sp.

Salps and doliolids

- Dolioletta gegenbauri
- Salpa fusiformis

Cirripede nauplius

- Lepas sp.

Copepods

- Aetideus armatus
- Calanus tenuicornis
- Ctenocalanus vanus
- Eucalanus crassus
- E. elongatus
- Euchaeta acuta
- Euchaeta tonsa
- Heterorhabdus papilliger
- Pleuromamma robusta
- Rhincalanus nasutus
- Sapphirina spp.
- Undeuchaeta plumosa

Thecosomes (Mollusca)

- Clio sp.

Figure 9a shows occurrences of the rare copepod Undeuchaeta plumosa in the North Atlantic Drift current while Fig. 9b illustrates the abundance of Calanus helgolandicus in the eastern parts of this current and over the European shelf. Clearly U. plumosa is restricted to oceanic waters. Calanus helgolandicus, by contrast, exists not only in neritic waters of the North Sea and eastern Atlantic shelf, but also in Drift waters well into the oceanic regime. Part c of Table 2 indicates that a variety of species occupy oceanic regions associated with Drift water.

Parathemisto gracilipes, though sharing waters occupied by Calanus helgolandicus, would appear to be found mostly in mixed water. Such is shown in the present study where Figs. 28 and 30-32 illustrate that this hyperiid was found rarely in Atlantic surface waters beyond the continental shelf and seldom in the purely neritic region of the southern North Sea. The boundaries of occurrence for P. gracilipes appear to be not unlike those for the copepod Candacia armata (Fig. 10a) which, nevertheless, differs from the amphipod in the distribution of abundance. Part d of Table 2 gives a good idea of the diversity of types that are variously distributed in oceanic and neritic regimes influenced by the North Atlantic Drift current.

There are a number of distributions overlying shallow-water regions which, in contrast to those which may either extend beyond the shelf or depend on oceanic intrusion, seem truly neritic in their requirements. Figure 10b shows,

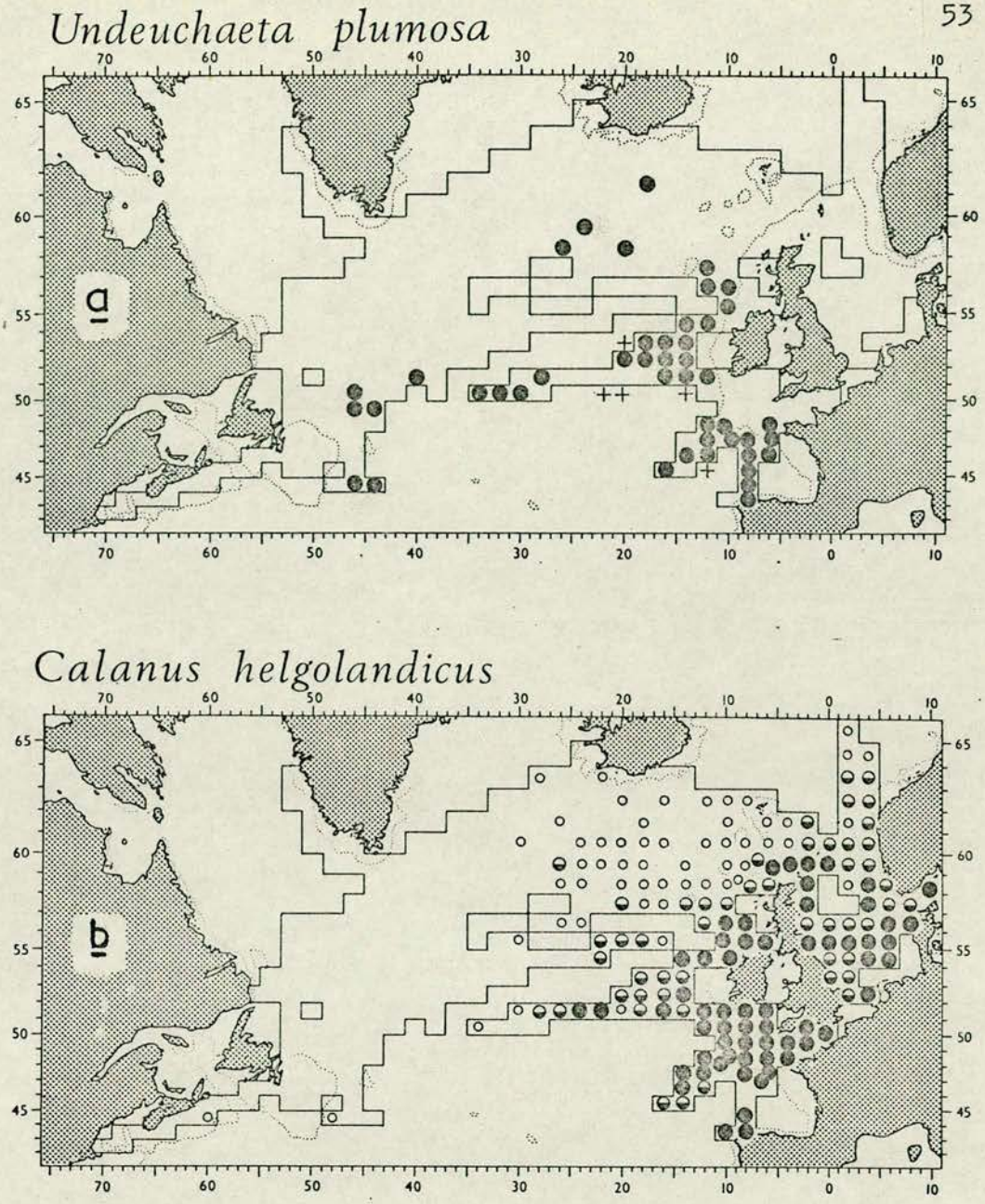

FIGURE 9 -- Preliminary charts from the Atlas of Plankton in preparation at the Oceanographic Laboratory, Edinburgh, showing distributions in surface waters during 1958-65: a, adults of the rare copepod Undeuchaeta plumosa (closed circles and plus signs showing presence in repeatedly and infrequently sampled areas, respectively) and b, adults of the copepod Calanus helgolandicus (open, half-closed and closed circles indicating rare, common and abundant densities, respectively). Region outlined includes only those statistical squares sampled frequently.

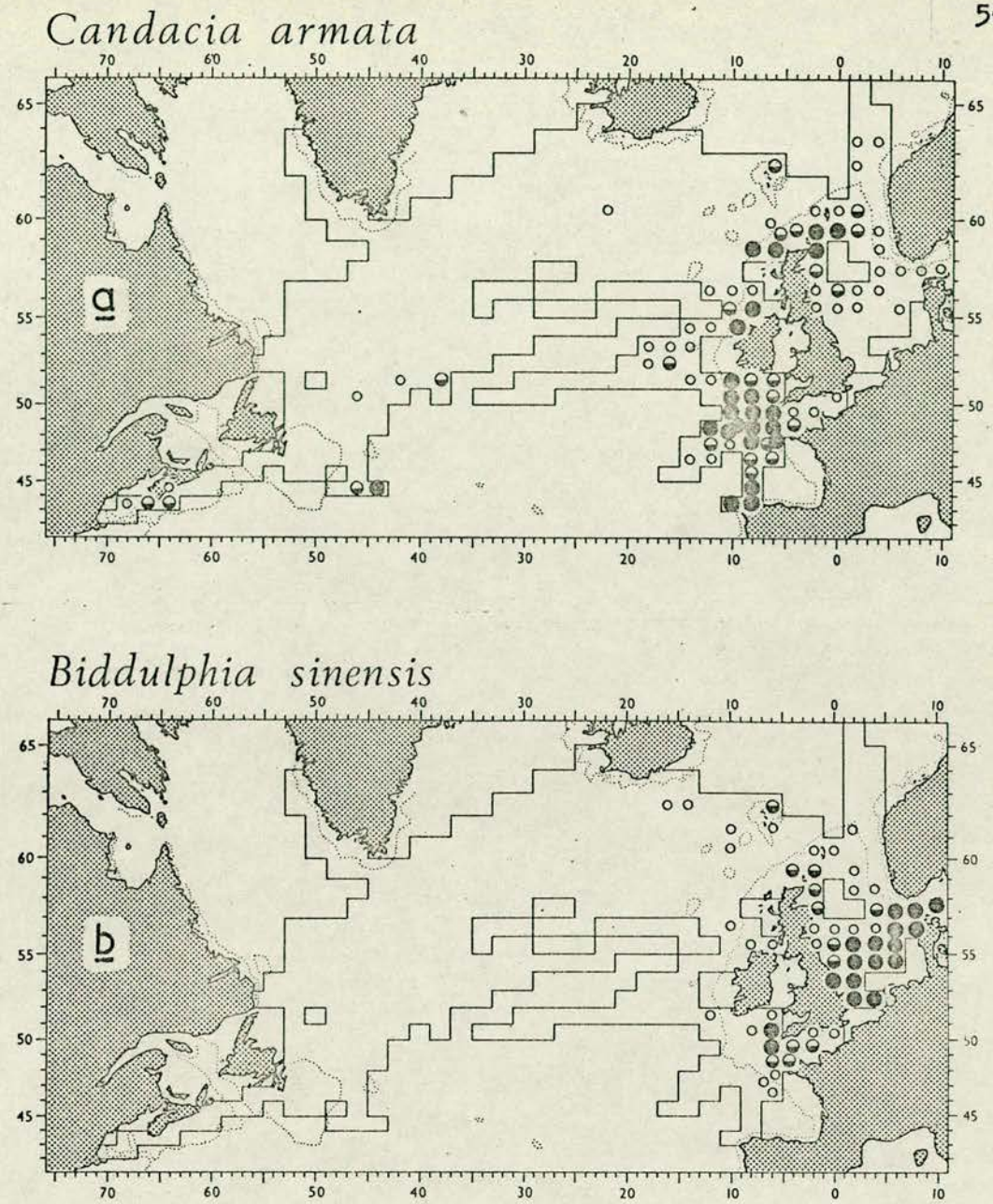

FIGURE 10 -- Preliminary charts from the Atlas of Plankton in preparation at the Oceanographic Laboratory, Edinburgh, showing distributions in surface waters during 1958-65: a, adults of the copepod Candacia armata and b, the diatom Biddulphia sinensis. Open, half-closed and closed circles indicate rare, common and abundant densities, respectively. Region outlined includes only those statistical squares sampled frequently.

TABLE 2 -- Part d.

NERITIC AND OCEANIC NORTH ATLANTIC DRIFT WATER

Diatoms

Asterionella japonica	*Rhizosolenia alata* var. *alata*
Hyalochaete spp.	*Skeletonema costatum*
Melosira sulcata	*Thalassionema nitschiodes*
Nitzschia seriata	

Dinoflagellates

Ceratium bucephalum	*C. longipes*
C. furca	*C. macroceros*
C. fusus	*C. tripos*
C. horridum	

Cladocerans

Evadne sp.	*Podon* sp.

Copepods

Acartia clausii	*Centropages typicus*
Anomalocera patersoni	*Euchaeta hebes*
Calanus finmarchicus helgolandicus	*Metridia lucens*
Candacea armata	*Paracalanus* spp.
	Pseudocalanus spp.

Thecosomes (Mollusca)

total (mainly *Spiratella*)

Diacria spp.

Hyperiids

Parathemisto gracilipes

for example, the distribution of *Biddulphia sinensis*. This diatom, which is abundant in the southern North Sea, is found beyond the shelf only north-west of Scotland, over the comparative shallows of the Wyville-Thomson Ridge and Iceland-Faeroe Rise. Figure 11a shows a similarly restricted distribution on the other side of the Atlantic where the neritic copepod *Tortanus discaudatus* would appear to exist primarily over the Grand Newfoundland Banks and shelf regions further south. The limited variety of taxa that are typical of open neritic conditions is illustrated in part e of Table 2.

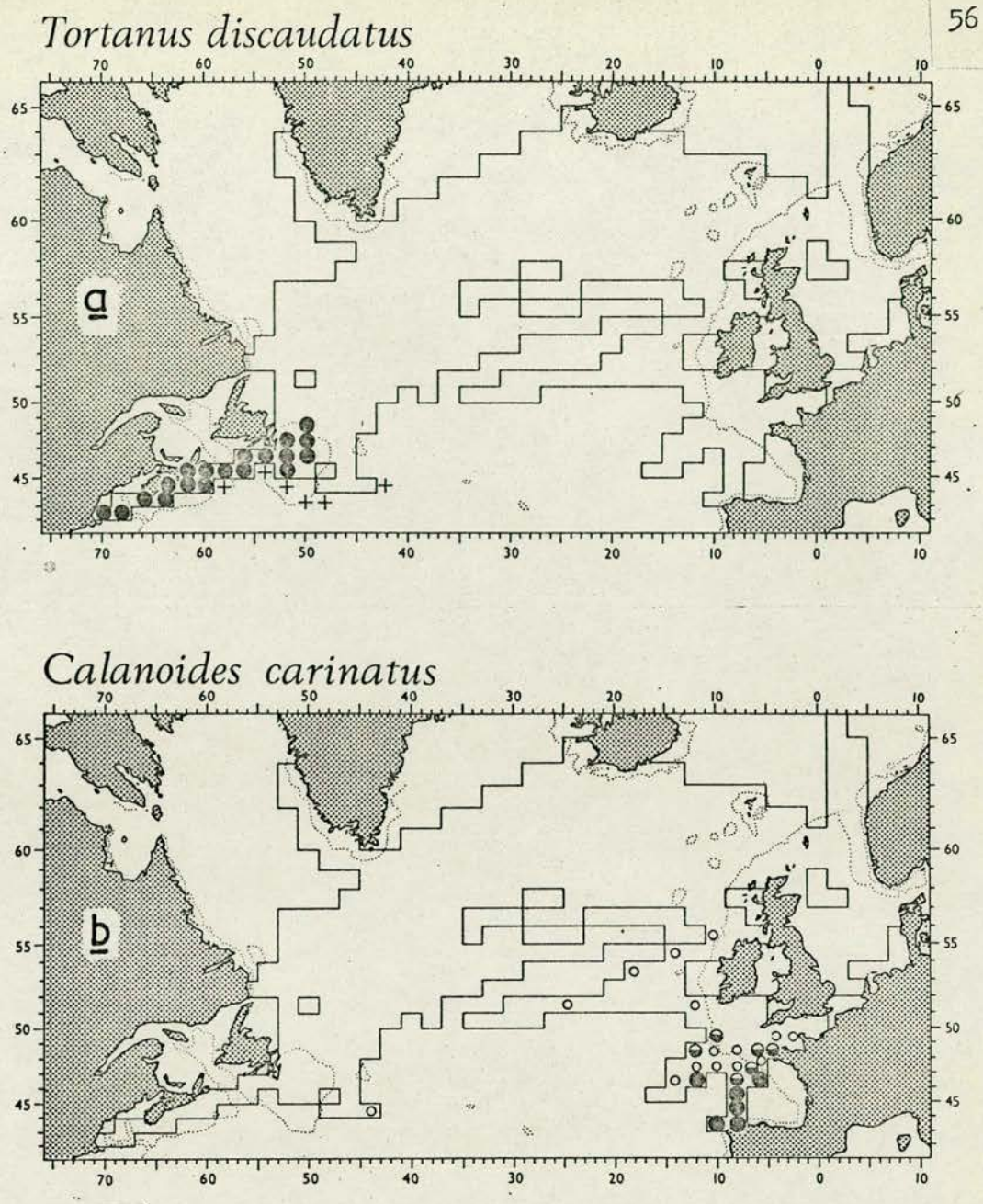

FIGURE 11 -- Preliminary charts from the Atlas of Plankton in preparation at the Oceanographic Laboratory, Edinburgh, showing distributions in surface waters during 1958-65: a, adults of the rare copepod Tortanus discaudatus (closed circles and plus signs showing presence in repeatedly and infrequently sampled areas, respectively) and b, adults of the copepod Calanoides carinatus (open, half-closed and closed circles indicating rare, common and abundant densities, respectively). Region outlined includes only those statistical squares sampled frequently.

TABLE 2 -- Part e.

NERITIC WATERS

(EUROPEAN SHELF)

Diatoms
- Biddulphia sinensis
- B. regia

Copepods
- Isias clavipes
- Labidocera wollastoni

(NORTH AMERICAN SHELF)

Copepods
- Tortanus discaudatus

(BOTH SHELVES)

Bryozoan larvae
- Cyphonautes spp.

Copepods
- Centropages hamatus
- Temora longicornis

Fishes
- Ammodytidae

Figure 11b shows the distribution of Calanoides carinatus, a warm-water copepod. Though it occurs widely over the warm Atlantic, its abundance off the Bay of Biscay suggests that it is primarily of Lusitanian origin. There are other species, relatively more numerous in the west, which show closer affiliation with water of the Gulf Stream. The long list of organisms associated in Table 2f with warmer waters is typical of the richness of species in the tropics and subtropics (Sverdrup et al., 1942; Fischer, 1960).

This table includes only organisms which occurred regularly and omits many species which were found but once or twice. The list associated with "warm Atlantic and Lusitanian water" might have been considerably more extensive therefore had all data been adequate for assigning distributions.

TABLE 2 -- Part f.

WARM ATLANTIC AND LUSITANIAN WATER[1]

Dinoflagellates

- Ceratium buceros
- C. candelabrum
- C. extensum
- C. gibberum
- C. karstenii
- C. massiliense
- C. pentagonum
- C. platycorne
- C. teres
- C. trichoceros

Salps and doliolids

- Doliolum mulleri
- D. nationalis
- Thalia democratica

Copepods

- Acartia danae
- Calocalanus spp.
- Calanoides carinatus
- Candacia pachydactyla
- Centropages bradyi
- C. chierchiae
- Clausocalanus arcuicornis
- Corycaeus anglicus
- Eucalanus attenuatus
- Euchaeta gracilis
- E. marina
- E. pubera
- Euchirella rostrata
- Haloptilus longicornis
- Iasis zonaria
- Lucicutia flavicornis
- Mecynocera clausi
- Nannocalanus minor
- Neocalanus gracilis
- Paracandacia bispinosa
- P. simplex
- Parapontella brevicornis
- Pleuromamma abdominalis
- P. borealis
- P. gracilis
- P. piseki
- P. xiphias
- Scolecithrix danae
- Temora stylifera
- Undeuchaeta major
- Undinula vulgaris
- Urocorycaeus spp.

Heteropods (Mollusca)

- Atlanta spp.

Certain taxa are widely distributed and numerous in a variety of different waters. In Table 2g these are located Under the heading "Various waters". At present it is difficult to allocate them to particular water bodies but no doubt, as their taxonomy becomes better understood (as it has for the Calanus finmarchicus complex of species and subspecies) it will be possible in future to distinguish a number of separate populations for each.

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[1]The term "Lusitanian" from Fraser, 1962.

TABLE 2 -- Part g.

VARIOUS WATERS[1]

Diatoms
- *Phaeoceros* spp.
- *Rhizosolenia hebetata* var. *semispina*
- *Rhizosolenia styliformis*
- *Thalassiosira* spp.

Chrysophytes
- *Phaeocystis* spp.

Copepods
- *Corethron hystrix*
- *Scolecithricella minor*

Gymnosomes (Mollusca)
- *Clione limacina*

Chaetognaths
- total (various species)

Polychaetes
- *Tomoperis* spp.

D6 Seasonal variations in the plankton

Organisms with similar geographical distributions are not necessarily part of each other's environment. To be so they must at least occur during the same season of the year. Possibly then they may be related in the food-chain, as competitors, predators or prey, as parasites or hosts.

As the number of species in subarctic water is relatively small (Table 2), it is easy to compare their seasonal cycles. Figure 12 shows some of these cycles expressed as percentages, by months, of the annual total for each taxon. All the cycles appeared over a similar period of the year but the rate of increase and the timing of seasonal maxima differed somewhat.

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[1] Under "Various waters" are listed taxa which are ubiquitous or difficult to allocate to particular water bodies.

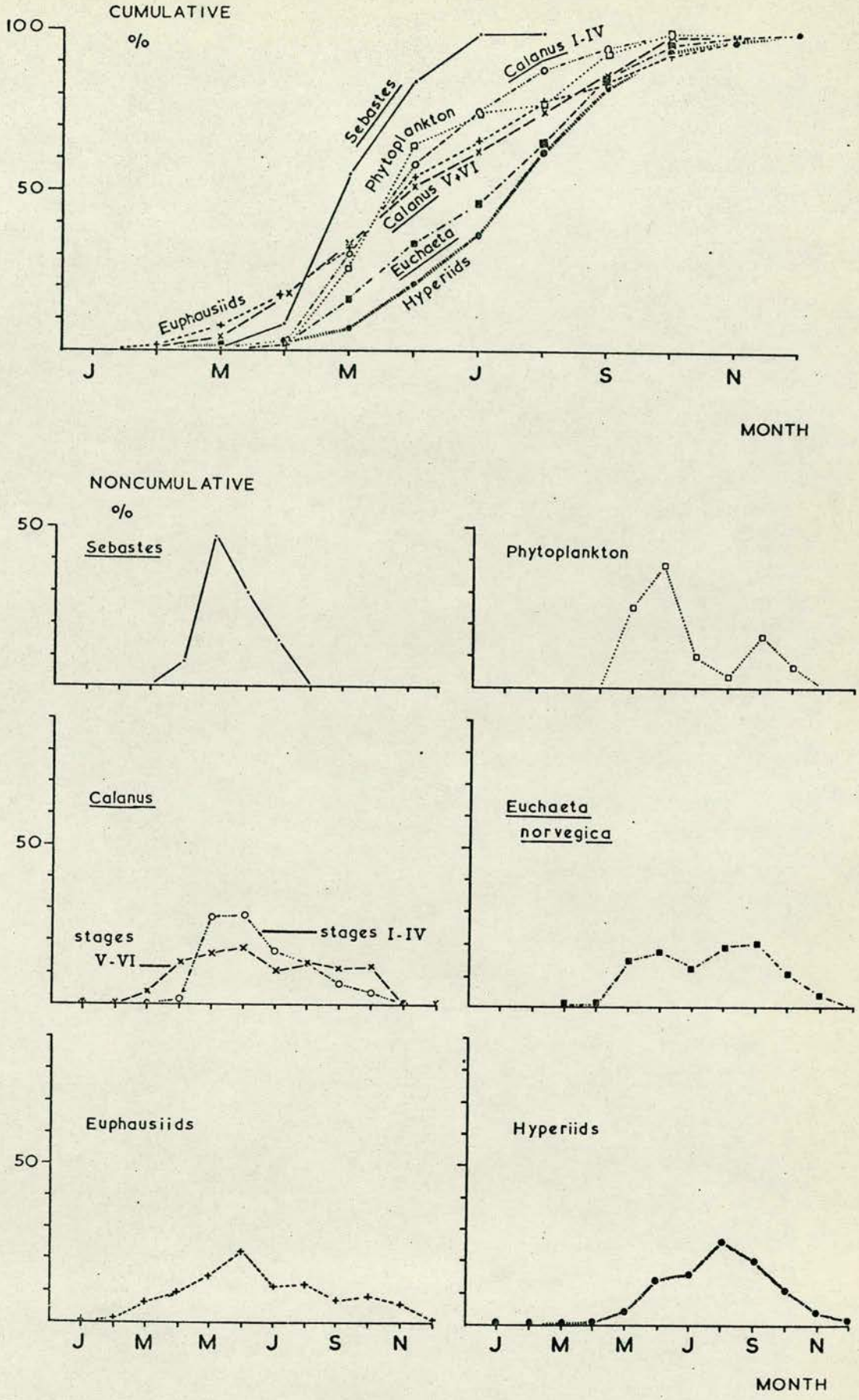

FIGURE 12 -- Legend on following page.

Though it may be observed that the earliest animals to appear were euphausiids and Calanus stages V and VI, the first to show an effective seasonal increase were larvae of the redfish Sebastes, half the total number of which were found by May (Fig. 12, cf. 50% cumulative). Next, along with the spring bloom of phytoplankton, were the adults (stages V and VI) and young (I-IV) of the copepod Calanus and the total of the euphausiids, all of which reached 50% of their annual sum by June. Finally, followed by the autumn flowering of phytoplankton, came the major increases of the copepod Euchaeta norvegica and the hyperiid amphipods.

FIGURE 12 -- Percentage monthly abundance of various organisms important in the subarctic surface waters of the North Atlantic, estimated from CPR samples taken from standard area B6 during the years 1962-5. Each graph, excepting that on the top, shows the monthly fluctuation in density of an organism (or a taxonomic group of organisms) in relation to the sum of observations for one year. That on the top (CUMULATIVE) indicates the proportion of the annual sum attained by any month. The amount of phytoplankton was determined as units of "phytoplankton colour", the intensity of which had been related by standards to the density of phytoplankton in the meshes of the filtering silk.

E METHODS OF ANALYSING THE HYPERIIDS

Hyperiids were examined in two ways: 1) Estimates from routine counting of plankton (to which I contributed my share), were analysed statistically for major variations in abundance. 2) A portion of samples were re-examined for composition of hyperiids in order to assess, wherever possible, those factors which might have influenced numbers. Consequently approximations were made describing distributions of taxa and indicating how abundance may vary in accordance with the response of the organism to variations in the environment.

E1 Statistics

Measurements of incidence were treated in two ways. Firstly the percentage of sampled standard areas with hyperiids present was examined for each month and, secondly, the percentage of sampled months with animals occurring was determined for each area. Thus, whereas temporal changes in the extent of geographical distribution are shown by investigation of incidence between months, places of persistent recurrence are indicated by comparison between areas. Furthermore, these places are illustrated by contours on charts of the North Atlantic and North Sea.

The contouring was based on a method kindly suggested to me by Dr A.I. Rees of Southampton University. In order to reduce personal bias, contours were determined rather

strictly on certain assumptions:

1) that the percentage for an area represents the incidence at a point at its centre,

2) that an interpolated percentage is representative of a point at the intercept of lines bordering adjacent areas, and

3) that the value, "x", at the intercept can be expressed as $x = \sum A/n_A$, where "A" is the percentage occurrence at an adjacent standard area and where "n" is the number of the A-values considered.

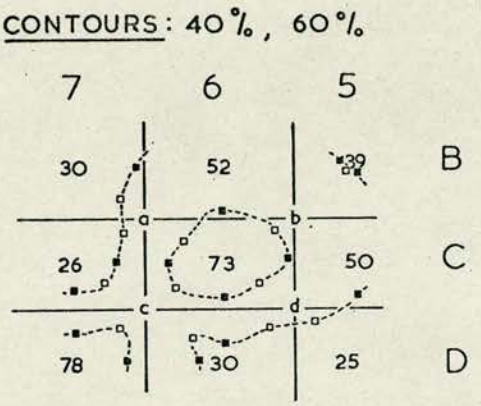

FIGURE 13 -- Example contours. Each is located on points estimated: 1) between centres of standard areas (closed squares), 2) between centres and intercepts of standard areas (open squares). The parameter, percentage incidence, whose distribution is so described, was initially determined as shown at the centre of each standard area and from these values, interpolated at the intercepts a, b, c and d (45, 54, 52 and 45%, respectively).

Where a percentage for "A" is missing, then percentages from nearby areas, "B", may be incorporated in the calculation $x = (\sum A + \frac{1}{2}\sum B)/(n_A + \frac{1}{2}n_B)$. However, to avoid determining a possibly unbalanced value, "x", for the intercept, wherever an "A" is missing and there are no percentages ("B") for nearby areas, then the A-value of the area opposite that without any value is omitted from the calculation $x = \sum A/n_A$.

Although these restrictions may introduce errors in location due to a geographical variation in sampling within standard areas, they are unlikely to give sufficient latitude for the expression of preconceived ideas. In this regard, the shape of distribution is considered more important than details of location.

The contours drawn are calculated at intervals representing 20, 40, 60, 80 and 90 per cent of the night-sampled months in which hyperiids were found to be present. An example of contouring is shown in Fig. 13.

Although variations in incidence may often be related to fluctuations in density, the two are not directly comparable. Whereas density measures the magnitude of a presence, incidence indicates its repetition. Incidence may suggest whether hyperiids are present widely or, consistently. Though information on the better sampled areas is lost by reducing data to "presence and absence", that from the poorly sampled peripheral regions can at least be considered.

The word "density" is used here to describe the number of specimens per unit of sampling (which theoretically may be related to a unit volume of sea-water sampled). "Abundance" on the other hand, is used in more general terms, without reference to the unit sampled (but not reserved, as is sometimes done, for expressing the total standing stock of a population, within which the density may vary).

As determined by the routine analysis of plankton, density is expressed as a "mean log value". The initial log values are derived from the category estimates (Table 1) of the relevant samples. The mean log value for "statistical squares" is taken to be the arithmetic mean of the original log values while that for "standard areas" is calculated as the arithmetic mean of the log values for constituent "statistical squares". Admittedly the mean log value for standard areas would be calculated more correctly using the first determined log values. The increase in calculation effort, however, would not improve the results noticeably.

To test for diurnal, seasonal and geographical differences in density, night and day densities were compared for the twelve months but data for the four years, 1962-5, were combined. To reveal seasonal and annual effects in individual areas, however, day densities were ignored and night values compared for the months of each year. The test employed was "analysis of variance", for which the observations must be independent, drawn from normally distributed

populations having similar variances and measured on an interval scale and, for which the effects must be additive (Siegel, 1956). Colebrook (1960) has shown that transformation to "log values" produces a statistical population which approaches normality. There seems no reason to suggest that the other conditions required by the test are not also approximated, though this would be difficult to demonstrate.

The standard areas to be examined for variations in abundance were selected mainly on the basis of sampling frequency during the years 1962-5. Of the 39 areas sampled at night over this period, 18 ranked higher than other areas, in the number of months sampled (being observed during at least 39 months, Table 3a) and one, area D7, though visited less frequently (for 31 months), was investigated at interals sufficiently close to allow for interpolation of missing values. As three of the 18 had hyperiids present too infrequently to be worthwhile considering (areas B1, B4 and C4 -- Table 3b), the total number of areas finally selected is sixteen. Despite a gap due to insufficient sampling between western areas and those to the north and east, this choice gives a fairly wide geographical coverage (Fig. 5b).

To indicate similarities of seasonal and annual abundance for hyperiids in different areas, correlation coefficients are calculated. For this, interpolated values for missing data were incorporated into the 4-year monthly means and the 12-month annual means. Where the pattern of associated areas was obvious, as between the seasonal

TABLE 3 -- Standard areas ranked according to the number of: a, months sampled at night and b, months in which night samples contained hyperiids.

a		b	
Areas	Months sampled	Areas	Months with hyperiids
C2	48	D8	40
B2 C1	47	C2	39
B4 B5	46	B5 B6	30
B1 D2 D4 D8	45	C1 E8	29
C5 D1	44	D7	28
B6 C4 D5 E9	43	C5	27
B7	42	E9	26
E4	41	C8	25
E8	39	D5	24
A6	37	B7	23
C7	36	D4	22
A1 D3	35	C6 D2 E10	21
C7	34	C7 D1	19
D7	31	B2 F8	18
E10	30	B4	17
C6	25	A6 E4	15
F8 F10	22	D9	14
D6	21	A1	13
E5	20	C4 D6	11
D9	16	F10	10
B8	12	B1 E5	9
E7 F7	9	D3 F4	7
A8	5	F7	5
F9	3	E7	4
E6	1	B8	3
		F9	2
		A8	1
		E6	0

correlations, coefficients (times ten, and rounded off to nearest whole number) are arranged in a matrix with highest values along the diagonal (Table 9); while those areas whose coefficients are generally low and negative in value and fail to fit well within the pattern, are relegated to the lower right. Though tests of significance are not applied to such coefficients since the data are serially related and therefore not independent (Colebrook and Robinson, 1964), it is noteworthy that those areas indicated to have their seasonal abundances highly correlated are the same ones implied by the analyses of variance to have had their monthly fluctuations statistically significant (cf. Tables 8 and 9).

To indicate temporal changes in the geographical distribution of abundance over the North Atlantic, "centres of distribution" are calculated.[1] This centre is the mean of all the latitudes and the longitudes for every standard area sampled, after each distance has been weighted by multiplying it by the average density. As a check against a biased distribution of sampled areas, their mean position, without weighting, is also determined. For each period in time both the centre of distribution and centre of sampling are plotted.

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[1]Figures 37-46 illustrate the use of these centres in summarizing the general position of distributions.

E2 Taxonomy

For analysis of hyperiid composition, all specimens were removed from the samples, examined microscopically, identified and counted. To devote a greater proportion of effort to studying Parathemisto, the genus whose numbers overwhelmingly dominate the variations in abundance, taxonomic work on other hyperiids is carried only as far as identification to genus or subgenus. This was facilitated principally by the use of an unpublished key and bibliography kindly loaned to me by Mr G.M. Spooner (Plymouth Laboratory). The bibliography led to a number of references which were used to supplement the key, especially with regard to illustrations. Those generally useful include:

Stebbing (1888)
Stephensen (1924)
Stephensen (1925)
Chevreux and Fage (1925)
Hurley (1955)

and others particularly valuable with regard to certain genera and subgenera are:

Pirlot (1939) -- juvenile Hyperoche
Bowman (1960) -- Parathemisto
Fage (1960) -- Rhabdosoma
Yang (1960) -- Hyperia (Parahyperia)
Bowman et al. (1963) -- Hyperia (Hyperia)

Specimens of Parathemisto over 3 mm in length and not too badly damaged were identified to species, or failing that, at least to some subgeneric classification. Those 3 mm

long or smaller were considered only as "Parathemisto species". Even when flattened, there were few specimens that could not be identified, at least to a certain extent.

In most cases there is no doubt whether specimens belong to one of the rare species, Parathemisto abyssorum or P. libellula. The common species P. gaudichaudii and P. gracilipes, however, can well be confused. Moreover, two forms exist for each of these common species, a long-legged or bispinosa form and a short-legged or compressa form (Stephensen, 1924). The bispinosa form of P. gracilipes is extremely rare in the present material (occurring only two or three times in about 327 positive identifications of the species) and therefore is unlikely to have been often mistaken for that of P. gaudichaudii. Difficulty is experienced, however, in separating a young stage of P. gaudichaudii form compressa from a stage of P. gracilipes insufficiently mature to have developed distinct secondary sexual characteristics. This difficulty arises because the two species are very similar morphologically, P. gracilipes being distinguished by the usually smaller size at maturity and the normally characteristic serrulation on the inner edge of the third uropod.

When a smallish specimen has not any secondary sexual character visible and the edge for the important serrulation of the third uropod is not clearly discernible (either because of flattening or insufficient morphological differentiation), there is no ready way of determining its

identity with certainty. To resolve the problem of having to dwell over such difficult decisions, an intermediate classification was devised, abbreviated as"Pcg", which represents any doubtful specimens which might, on morphological grounds, be assigned to either Parathemisto gaudichaudii form compressa or P. gracilipes.

Previous works have named a variety of morphological features as useful for the separation of Parathemisto gaudichaudii and P. gracilipes. Many of these characters, however, were found in the present material to vary widely between individuals. For example, the proportional differences of pereopod 2 suggested by Hurley (1955 - his gnathopod 2), fluctuate with size of specimens and the relative lengths of pereopods 5-7 referred to by Dunbar (1963) were found to differ with sex. One distinctive feature described by Sars (1895) for P. abyssorum (as P. oblivia), on the other hand, seems not to have been mentioned since. The lack of distal setae on the basal part of the maxilliped was found to be a diagnostic feature, particularly for identification of the very large specimens which were often damaged. Even by the head alone, the species could be recognized.

The key in Table 4 summarizes the criteria by which the species of Parathemisto are separated in the present study. Figure 8 gives a generalized sketch for location of appendages mentioned in the key while Fig. 9 (a - k) illustrates certain characteristic features present on some of these appendages.

TABLE 4 -- Key[1] to identification of the species of Parathemisto from the North Atlantic (prepared and adapted by the author for the present study from characteristics indicated in Sars, 1895; Barnard, 1930; Hurley, 1955; and Bowman, 1960).

1(2) Pereopod[2] 5 slightly shorter than pereopod 7[3]; posterior (ventral) edge of carpus of pereopod 3 and 4 nearly straight (Fig. 9a); basal part of maxilliped without distal setae (Fig. 9b) . . . . Parathemisto abyssorum

2(1) Pereopod 5 longer than pereopod 7 and other pereopods; posterior edge of carpus of pereopod 3 and 4 convex (Fig. 9, f and k); basal part of maxilliped with one or more setae (Fig. 9g).

3(4) Base of dactyl of pereopods 5-7 with setae (Fig. 9c) . . . . P. libellula

4(3) Base of dactyl of pereopods 5-7 without setae (Fig. 9h).

5(6 or 7) Inner margin of endopodite of uropod 3 distinctly serrulate (Fig. 9d) . . . . . P. gracilipes

6(5 or 7) Inner Margin of endopodite of uropod 3 indistinct, often because of lateral flattening. (Characteristics of P. gaudichaudii form bispinosa not present. See Table 4.) Intermediate classification . . Pcg (= P. gaudichaudii form compressa or P. gracilipes form compressa)

7(5 or 6) Inner margin of endopodite of uropod 3 relatively smooth (Fig. 9i) . . . . . P. gaudichaudii

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[1]Agreement of description with a specimen gives the species whereas disagreement leads to the alternative, numbered in parentheses.

[2]The spelling "pereopod" rather than "peraeopod" or "periopod" is defended by Wolff (1962) and recommended by Bowman (personal communication, 1967).

[3]Ratio of pereopod lengths given in Behning (1939) and Bowman (1960) for Parathemisto abyssorum as 5>7>6 are in error and should have been 7>5=6 (Shen, MS 1966; Bowman, 1967 - personal communication).

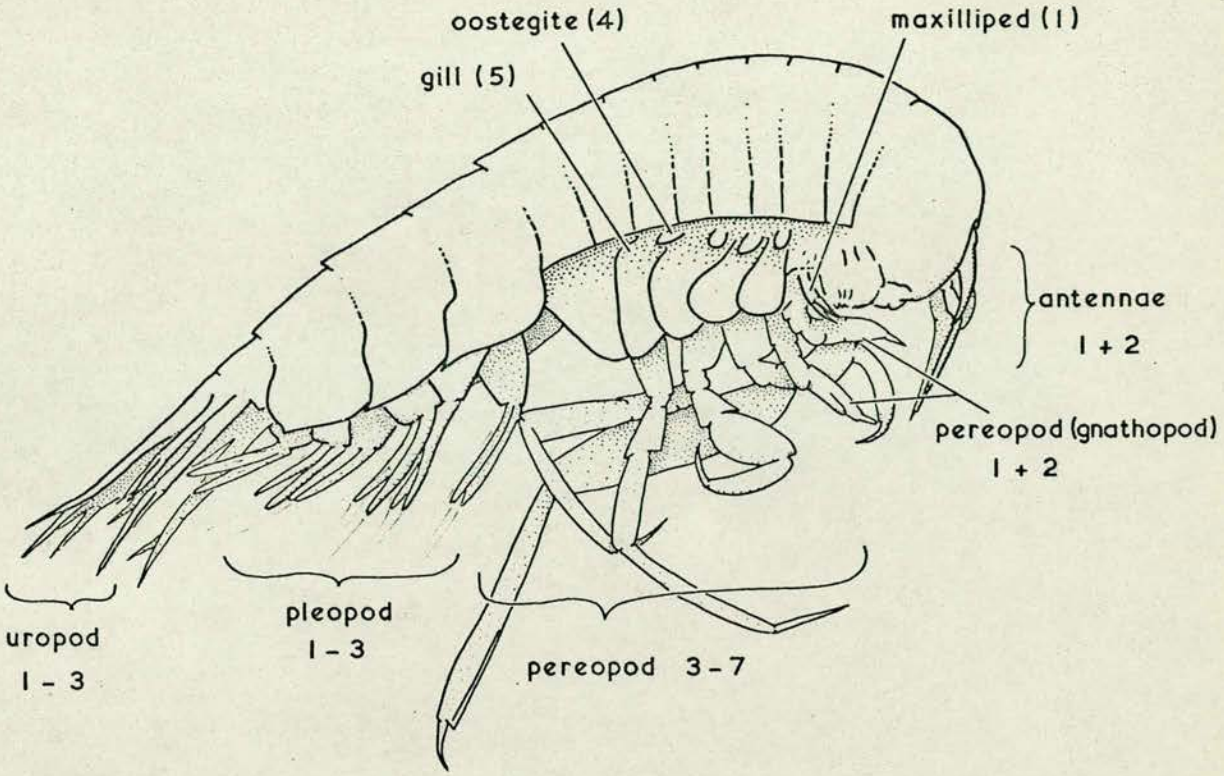

FIGURE 14 -- Generalized sketch drawn by the author from a prepuberty-stage female of Parathemisto gaudichaudii form compressa, with right pereopods removed to show, on the left, four rudimentary oostegites and five gills.

E3 Size, form and maturity

For precise determination of size, the lengths of specimens were measured under the microscope to the nearest twelfth of a millimetre (unit of eyepiece micrometer) and combined into categories one millimetre long (eg., 1.0-1.9 mm, 2.0-2.9 mm, etc.). Each length was taken from the foremost part of the head (not including antennae) to the tip of the third uropod. Since specimens are often inflexibly

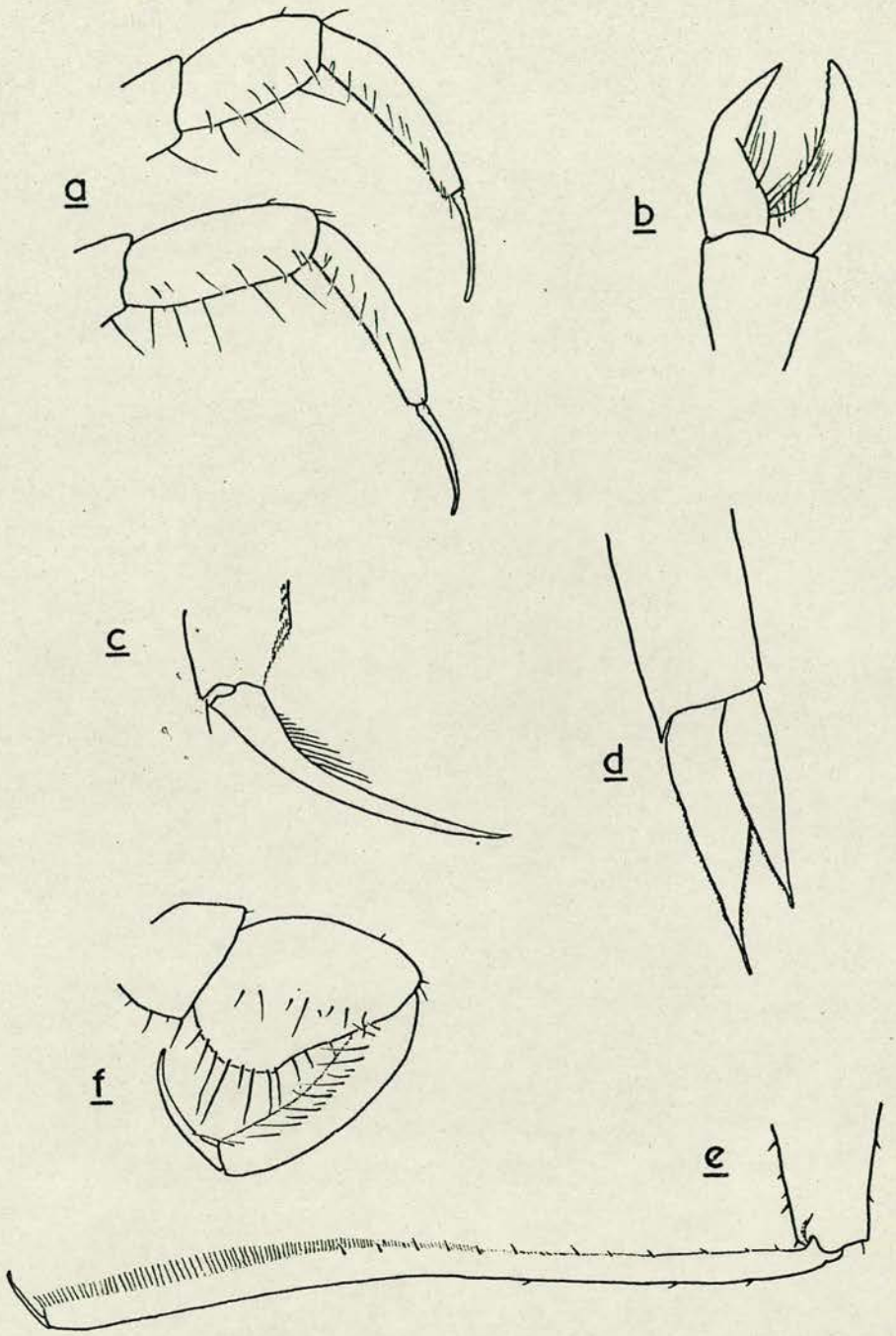

FIGURE 15 -- Legend on following page; continued.

FIGURE 15 -- Taxonomic characters for:

Parathemisto abyssorum Boeck (prepuberty-stage male, 14.3 mm long, from Barents Sea -- drawings by the author from a specimen obtained courtesy J. Corlett, Lowestoft) --

a, part of pereopods 3 and 4, showing carpus of each (carpus = third segment from end), medial view.

b, maxilliped showing absence of distal setae on basal part, postero-ventral view.

Parathemisto libellula Lichtenstein (juvenile, 7.2 mm long, from Davis Strait by DANA on Norwestlant Survey 3 -- drawing by the author from a specimen obtained courtesy V. Bainbridge, Edinburgh) --

c, part of pereopod 7 showing setae at base of dactyl, medial view.

Parathemisto gracilipes (Norman), (puberty-stage male, 7.9 mm long, from North Sea -- drawing by the author from a specimen obtained courtesy F. Evans, Cullercoats) --

d, part of uropod 3 showing serrulation on inner margin of endopodite (i.e. left margin of left ramus), ventral view.

Parathemisto gaudichaudii (Guérin) form bispinosa (prepuberty-stage male, 12.1 mm long, from southern Norwegian Sea east of Faeroe -- drawings by the author from a specimen obtained courtesy J. Fraser, Aberdeen) --

e, part of pereopod 5 showing comb of setae on propod, medial view.

f, part of pereopod 3 showing proximal position of widest point on carpus, medial view.

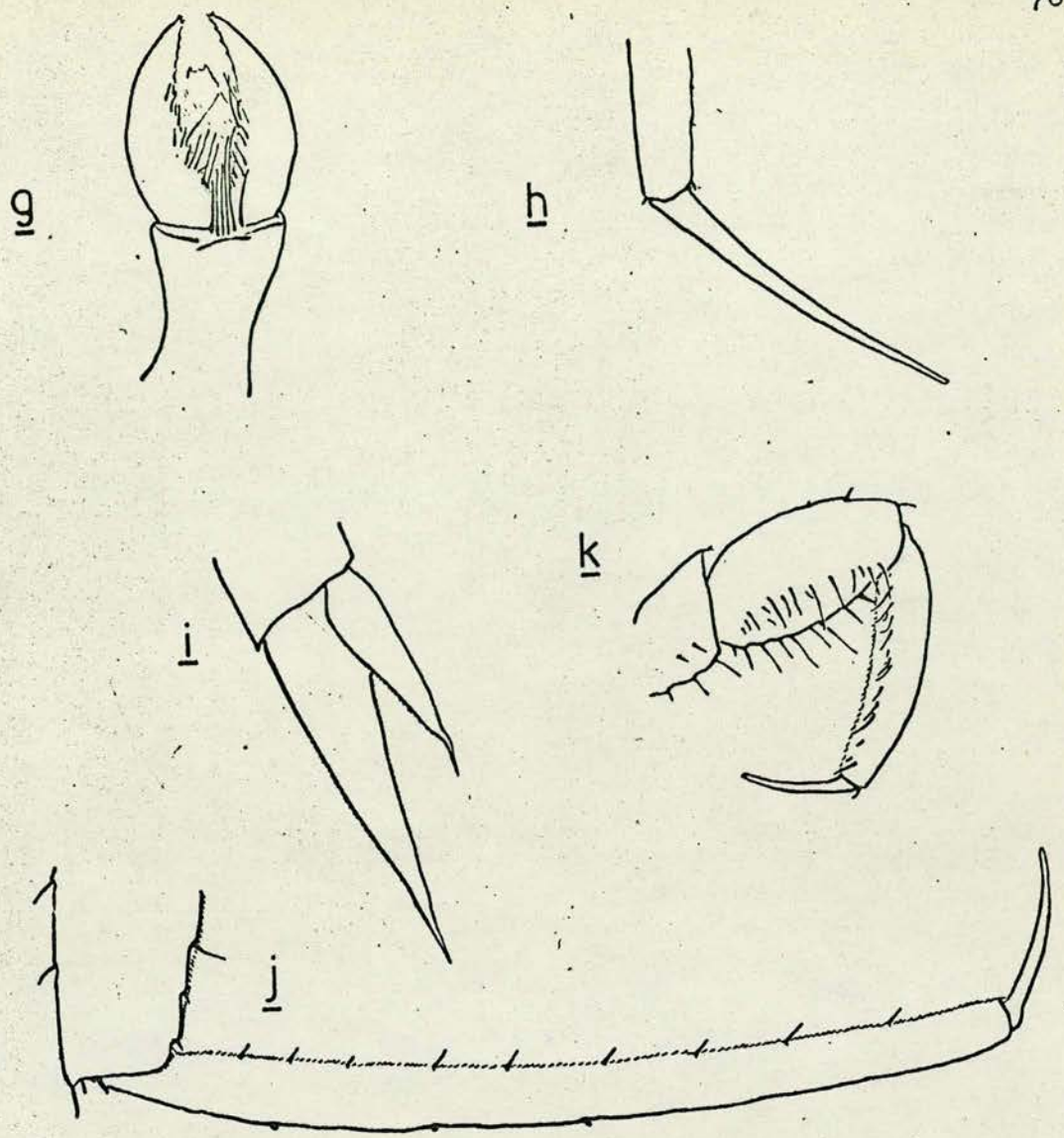

FIGURE 15 -- Taxonomic characters, continued:

Parathemisto gaudichaudii (Guerin) form compressa (prepuberty-stage male, 14.6 mm long, from 53°25'N, 34°00'W by DANA on Norwestlant Survey 3 -- drawings by the author from a specimen obtained courtesy V. Bainbridge, Edinburgh)--

g, maxilliped showing presence of distal setae on basal part, postero-ventral view.

P. gaudichaudii compressa (puberty-stage female, 20.9 mm long, from 57°42'N, 37°15'W by ANTON DOHRN on Norwestlant Survey 2 -- drawings by the author from a specimen obtained courtesy V. Bainbridge, Edinburgh) --

h, part of pereopod 7 showing absence of setae at base of dactyl.

curved to different degrees, the measurement was taken along the midline by accumulating a series of short measures.

By this procedure, lengths of Parathemisto gaudichaudii are considered in relation to time of day, season, year and geographical area.

The material examined was collected in April, July, September and November of the years 1962-5, the particular months being chosen with reference to a joint study within the Oceanographic Laboratory (on biomass of plankton, reported under Biogeography, Scottish Mar. Biol. Assoc., 1968). The standard areas from which this was taken, B6 and D8, were not only well sampled and persistently populated, but also showed an interesting difference between one another in the timing of seasonal abundance.

Entire samples were examinated until at least 10 specimens were measured for each combination of time of day, month, year and area or until specimens from all available samples for a combination (including the alternative ones usually not analysed) had been considered. Because of the limited availability of specimens for some combinations and the relatively long time consumed by these rather precise measurements, a greater number of determinations was impractical.

Initial exploration of the CPR material included not only a quick determination of size but also an assessment of ontological development in certain external features by which

the species, forms and sexes of Parathemisto are separated. The samples examined were taken at night from standard areas B5 throughout 1965 and, both night and day from routes Gd and Nb through 1962-5 and 1963-5, respectively (collection along route Nb began in 1963). As these particular parts of the collection are neither seasonally biased nor composed of many hyperiids other than Parathemisto gaudichaudii, the data gathered is particularly suitable for comparing size and maturity within the species.

For the quick determination of size, specimens are sorted by eye into four broad categories of length divided at approximately 3, 7 and 12 mm. Such a crude method proved adequate except where an accurate estimate of average or modal length was required.

Besides the distinctly bispinosa and compressa forms of Parathemisto gaudichaudii, specimens occur with distinguishing features which are: 1) lost, 2) morphologically intermediate in character or 3) morphologically some mixture of the extreme characteristics. To accommodate these specimens of difficult determination, an intermediate classification (abbreviated "Pbc") is adopted. A selection of those features indicated by Sars (1895), Stephensen (1924) and Mogk (1927) to separate these extreme and intermediate forms are summarized by the key in Table 5.

Altogether five classifications of Parathemisto gaudichaudii have evolved for the purposes of the present study. "Psp" includes specimens of 3 mm long or smaller,

TABLE 5 -- Key to identification of the forms of Parathemisto gaudichaudii including provision for an intermediate classification (prepared and adapted by the author for the present study from characteristics indicated in Sars, 1895; Stephensen, 1924; and Mogk, 1927).

1(2 or 3) Propus of pereopod 5 with comb of setae gradually becoming very high distally (Fig. 9e); carpus of pereopod 3 widest just proximal to its centre (Fig. 9f) . . . Parathemisto gaudichaudii form bispinosa.

2(1 or 3) Propus of pereopod 5 with comb of setae more or less even and low (Fig. 9j); carpus of pereopod 3 widest near its centre (Fig. 9k) . . . . . P. gaudichaudii form compressa.

3(1 or 2) Propus of pereopod 5 and carpus of pereopod 3 of intermediate or mixed character. Intermediate classification . . Pbc (= P. gaudichaudii form bispinosa or form compressa or actual intermediate).

"Pcg" accommodates those of the compressa form which are larger but confusable with P. gracilipes while "Pb", "Pc" and "Pbc" refer to those definitely recognized as P. gaudichaudii and further separable as the extreme forms, bispinosa and compressa, or their intermediates.

From a portion of the samples analysed, the relative numbers of Parathemisto gaudichaudii in the five classifications of development were estimated for each month and each standard area. Densities represented were then subdivided accordingly and a mean log value was

determined for each category. Although the various categories do represent steps in the growth process, they are not equal ones. The least developed specimens (Psp), for example, are represented within the narrow range of about 2 mm (from 1.0 to 2.9 mm) whereas the better differentiated ones are expressed in much wider spans in the order of 10 mm (for Pcg) and 16 mm (for Pc+Pbc+Pb) (see Fig. 29 for analysis of size).

In order to compare the relative numbers of specimens of different sizes, therefore, it was necessary to adjust those data related to morphological differentiation. Values related to the average density per millimetre were produced by dividing density values for each category by the appropriate number of millimetres represented. By this procedure, information on the development of specimens was converted to give a rough indication of the length frequency distribution.

For the expression of geographical distribution these adjustments are not made and therefore comparison between categories is not legitimate, except perhaps between those for which the ranges of size are nearly equal (i.e., bispinosa and compressa). Where the relative abundance for stages in growth is compared over the seasonal cycle, however, adjustment of values is a necessity.

Specimens examined for seasonal variation are from the night collections of seven months -- January, March, May, July, August, September and November -- in the year 1965. Those observed for annual variation are from night samples taken during August and September of the four years,

1962-5. Though examination of more samples from years 1963-5 might have shown whether seasonal changes varied between years, time unfortunately did not allow for the additional work.

Kane (1963) describes the development of secondary sexual characteristics in Parathemisto gaudichaudii and shows that in the female it proceeds in accordance with growth of the ovary. Features used in the present study to indicate maturity or its approach are 1) the presence of segmentation of the antennal flagellae in the male and 2) the existence of oostegites in the female. Though the search required to see the transparent rudimentary oostegite of the female in prepuberty (Fig. 8) is often time consuming, these characters are not too difficult to determine.

F RESULTS

F1 Distribution of hyperiids in general

F1.1 Variations of incidence

Though present everywhere over the North Atlantic Ocean, hyperiids varied in occurrence depending on the season and the year. On average, for the years 1962-5, they became increasingly widespread through the spring and summer until about October when they inhabited more than 75% of the area of surface waters sampled. After this maximum dispersal they rapidly disappeared from most regions, being found in only 33% of the region in January (Fig. 16a). Figure 16b suggests that spread of occurrence increased also with the years, more noticeably from 1962 to 1964 than from 1964 to 1965. Despite this year-to-year variation, the seasonal trend toward greater spread in "summer-autumn" (June to November) than in "winter-spring" (December to May) remained characteristic (Fig. 16c).

With seasonal and annual variations in geographical dispersal, the occurrence in particular areas showed fluctuation. Table 6 gives the percentage incidence within each standard area, along with the months of sampling and months of incidence. With few exceptions (in 1962-3, areas

TABLE 6 -- Percentage of months (%)[1] in which hyperiids were present in the surface water of each standard area. Calculated from the number of months sampled at night (S) and the number in which hyperiids were present (P).

	1962-3						1964-5					
	Jun-Nov			Dec-May			Jun-Nov			Dec-May		
Area	S	P	%	S	P	%	S	P	%	S	P	%
A1	10	3	30	7	1	14	9	7	78	9	3	33
A6	8	6	75	12	2	17	8	7	88	9	0	0
A7	4	3	75	5	1	20	7	6	86	2	0	(0)
A8	1	0	(0)	1	0	(0)	2	1	(50)	1	0	(0)
B1	12	3	25	11	1	91	11	5	45	11	0	0
B2	12	6	50	11	5	45	9	7	78	12	0	0
B4	11	3	27	12	2	17	11	8	73	12	4	33
B5	12	12	100	12	4	33	12	11	92	11	5	45
B6	10	9	90	12	6	50	12	11	92	9	5	56
B7	11	9	82	10	4	40	10	8	80	10	2	20
B8	7	0	0	2	1	(50)	3	2	67	2	1	(50)
C1	12	9	75	12	6	50	12	8	67	12	7	58
C2	12	7	58	12	9	75	12	11	92	12	12	100
C4	10	6	60	11	2	18	10	3	30	12	1	8
C5	8	6	75	11	3	27	12	10	83	11	8	73
C6	6	6	100	3	2	67	8	7	88	8	6	75
C7	8	6	75	8	2	25	9	8	89	11	3	27
C8	12	12	100	5	2	40	10	9	90	7	3	43
D1	11	6	55	12	6	50	10	4	40	12	3	25
D2	9	3	33	11	3	27	11	10	91	12	5	42
D3	5	1	20	11	2	18	10	2	20	9	2	22
D4	11	9	82	11	4	36	11	5	45	11	4	36
D5	12	9	75	10	1	10	11	10	91	10	4	40
D6	5	3	60	5	2	40	6	5	83	5	1	20
D7	7	7	100	8	6	75	7	7	100	10	8	80
D8	11	11	100	10	7	70	12	12	100	11	10	91
D9	7	7	100	1	1	(100)	6	6	100	2	0	(0)
E4	11	6	55	10	1	10	10	5	50	9	3	33
E5	4	2	50	7	2	29	3	2	67	6	3	50
E6	0	0	(-)	0	0	(-)	0	0	(-)	1	0	(0)
E7	1	1	(100)	2	2	(100)	1	0	(0)	5	2	40
E8	7	6	86	10	5	50	10	9	90	12	10	83
E9	11	5	45	11	4	36	10	8	80	10	9	90
E10	8	7	88	6	2	33	7	7	100	9	5	56
F4	8	1	13	9	0	0	10	3	30	7	0	0
F7	3	2	67	0	0	(-)	5	3	60	1	0	(0)
F8	4	3	75	1	0	(0)	8	8	100	7	7	100
F9	0	0	(-)	0	0	(-)	1	1	(100)	2	1	(50)
F10	8	5	63	4	0	0	5	4	80	5	1	20

[1]Parentheses indicate percentages where fewer than three months of sampling were available for calculation.

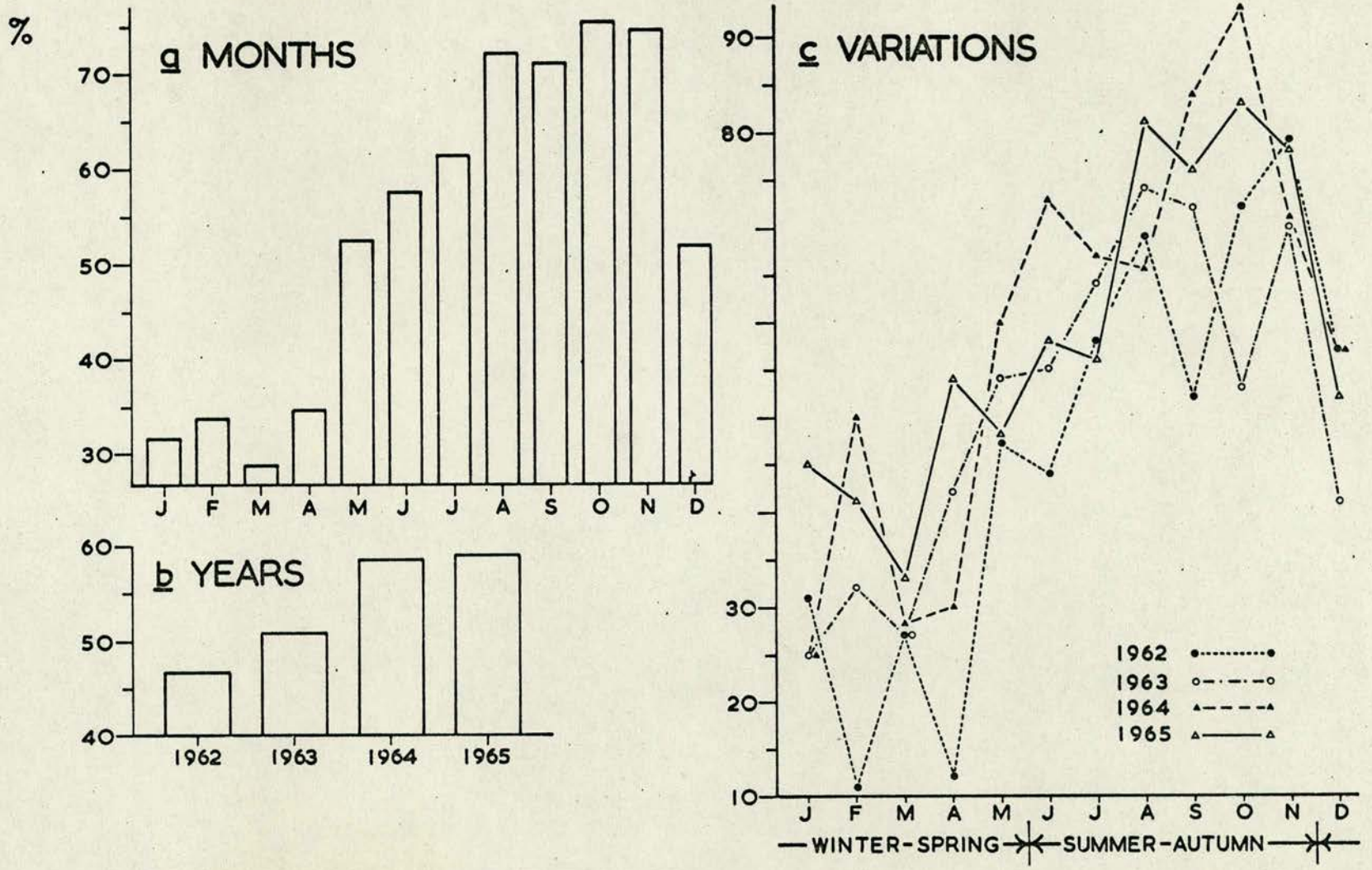

FIGURE 16 -- Legend at foot of following page.

B1 and C2; in 1964-5, areas C2, D3 and E9), the animals occurred in more of the months of June to November than in those from December to May. On the other hand, biennial increases in appearance, from 1962-3 to 1964-5, were limited geographically. When incidence is compared separately for winter-spring and summer-autumn periods, increases are shown to have occurred in only two thirds of areas, for either period. For both seasonal intervals, increases occurred in no more than half of the areas; animals in other regions appeared in 1964-5 at the same or at a lesser frequency compared to 1962-3. Thus, whereas a seasonal increase in the appearance of animals is a consistent feature for a large part of the North Atlantic, an annual (or a biennial) rise is not general.

F1.2 Geographical patterns of incidence

There was a clear geographical pattern in the incidence of hyperiids which was basically similar in winter-spring and summer-autumn. Figure 17 (a and b) shows two major regions where occurrence was frequent, one oceanic in subarctic water and one neritic in the northern

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FIGURE 16 -- Percentage of geographical spread of hyperiids in surface waters, estimated from samples taken at night during the years 1962-5. The proportion of the standard areas sampled which possessed hyperiids is indicated for: a, months; b, years and c, month-by-year variations.

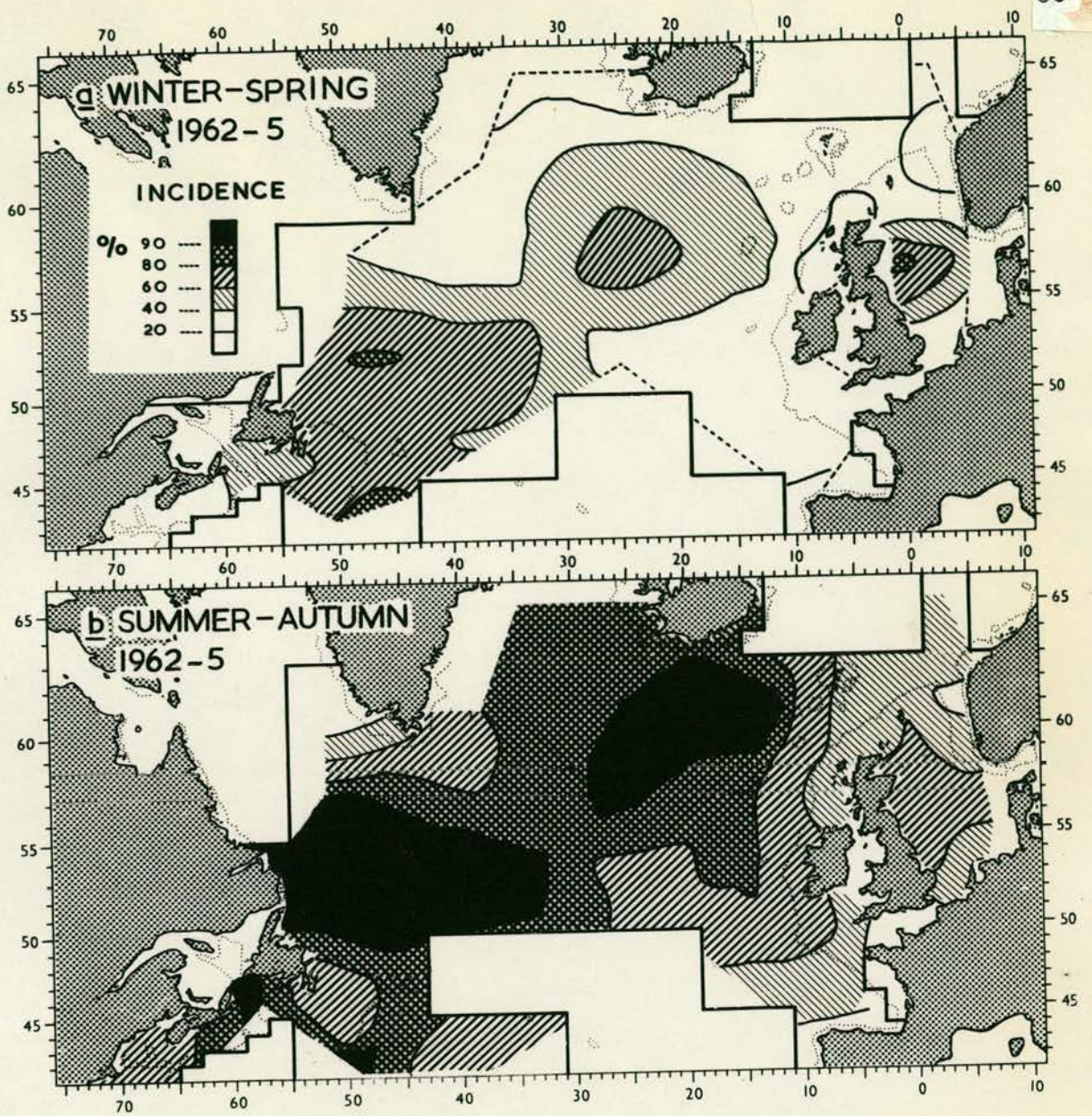

FIGURE 17 -- Geographical distribution of the incidence of hyperiids in surface waters during the years 1962-5, shown for the seasonal periods: a, winter-spring; b, summer-autumn. Incidence expressed as the percentage of months sampled at night in which hyperiids were found to be present.

North Sea. Incidence in the subarctic region was especially persistent at centres north-east of Newfoundland and south of Iceland while in the North Sea it was highest at a centre rather closer to the British coast than to the continent.

There were minor seasonal differences in the basic geographical pattern for incidence. For example, in the warm season both the subarctic centres of incidence were slightly to the north of their positions during the cold season. Moreover, in the warm season hyperiids were present west of Iceland, south-west of Nova Scotia and south-west of Ireland where they rarely occurred in winter-spring. In other words, during the warmer months their distribution extended both northward and southward, but most obviously to the north (cf. a and b, Fig. 17). These extensions account for a good portion of the increased geographical spread previously indicated for the months of summer and autumn (Fig. 16a).

The areas in which hyperiids appeared seldom were: the southern North Sea and English Channel, regions west of Norway, west of Spain and, perhaps (though not sampled in winter-spring), west of Greenland. At only two places were hyperiids consistently infrequent: in the English Channel and off the west of Spain. In other places where incidence was generally low (eg. west of Greenland, west of Norway and in the southern North Sea), they showed a more variable appearance (Fig. 18). Over the Grand Banks of Newfoundland

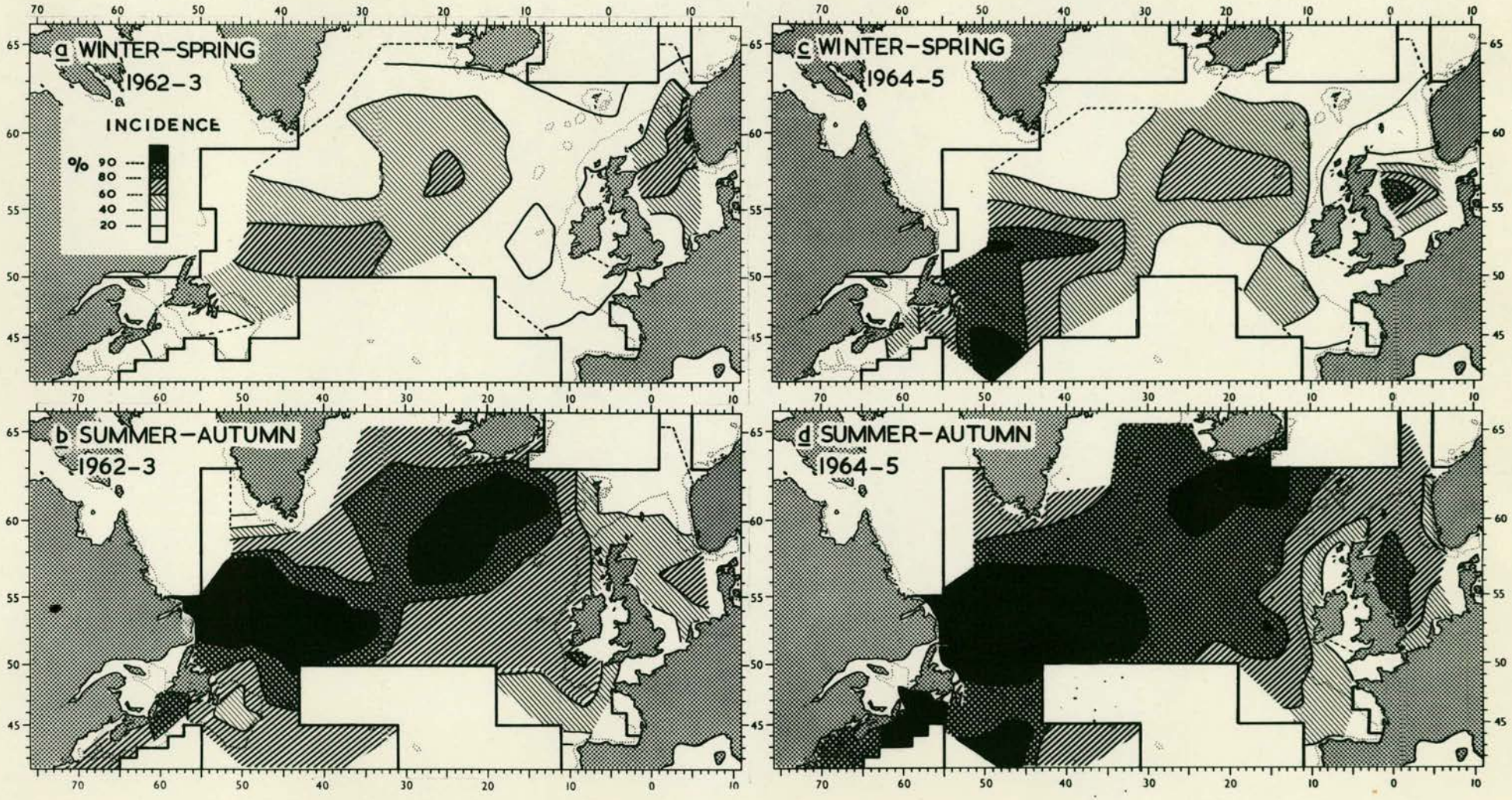

FIGURE 18 -- Legend at foot of following page.

there appeared a curious pattern in summer-autumn. At this time hyperiids were less common than in adjacent areas around the Bank (Fig. 17).

The patterns of distribution illustrated in Fig. 17 are based on the average incidence in the standard areas during the four years 1962-5. Division of the results into the two biennial periods (1962-3 and 1964-5) does not show any major departures from the generalized patterns (cf. Fig. 18). In the open ocean the main centres of incidence in the subarctic region are clearly shown north-east of Newfoundland and south of Iceland though they both tend to be further north in summer-autumn of 1964-5 than in 1962-3. The centre in the North Sea again appears to the north. There is a suggestion, however, that its position may have shifted, being perhaps closer to the continent in 1962-3 than in 1964-5.

F1.3 Variations of abundance

Sources of variation affecting the abundance of hyperiids were assessed by the analysis of variance. The results in Table 7 show that the diurnal effect (D)

FIGURE 18 -- Geographical distribution of the incidence of hyperiids in surface waters, for the seasonal and biennial combinations:

a, winter-spring, 1962-3; b, summer-autumn, 1962-3;
c, winter-spring, 1964-5; d, summer-autumn, 1964-5.

TABLE 7 -- Analysis of variance to show the effects of time of day, month, and area on the density of hyperiids in the surface water. Level of statistical significance implied (but not verified) : * = 5%, ** = 1%.

	df	MSS	%MSS
Diurnal (D)	1	278,587**	81.4
Month (M)	11	23,552**	6.9
Area (A)	15	17,945**	5.2
D x M	11	9,222**	2.7
D x A	15	9,571**	2.8
M x A	165	2,030**	0.6
Total	383		
Error	165	1,190	0.3

accounted for 81.4% of the total variation, while variation attributable to months (M), areas (A) and their interaction (M x A) amounted to 6.9, 5.2% and 0.6%, respectively.

As reflected in the "Areas" variance, hyperiids were more abundant in some places than in others. Figure 19 indicates that more animals were present in subarctic water than in water of the North Sea and North Atlantic Drift (cf. Fig. 1). The interactions in Table 7 (D x A, M x A), however, show that this geographical pattern differed temporally. Thus, the interpretation of the survey results must take account of the time of sampling.

Hyperiids taken by night were always on average more abundant than by day, in the surface waters sampled with the CPR. Though this is the case for all areas (cf. white and shaded columns, Fig. 19) and for all months (see

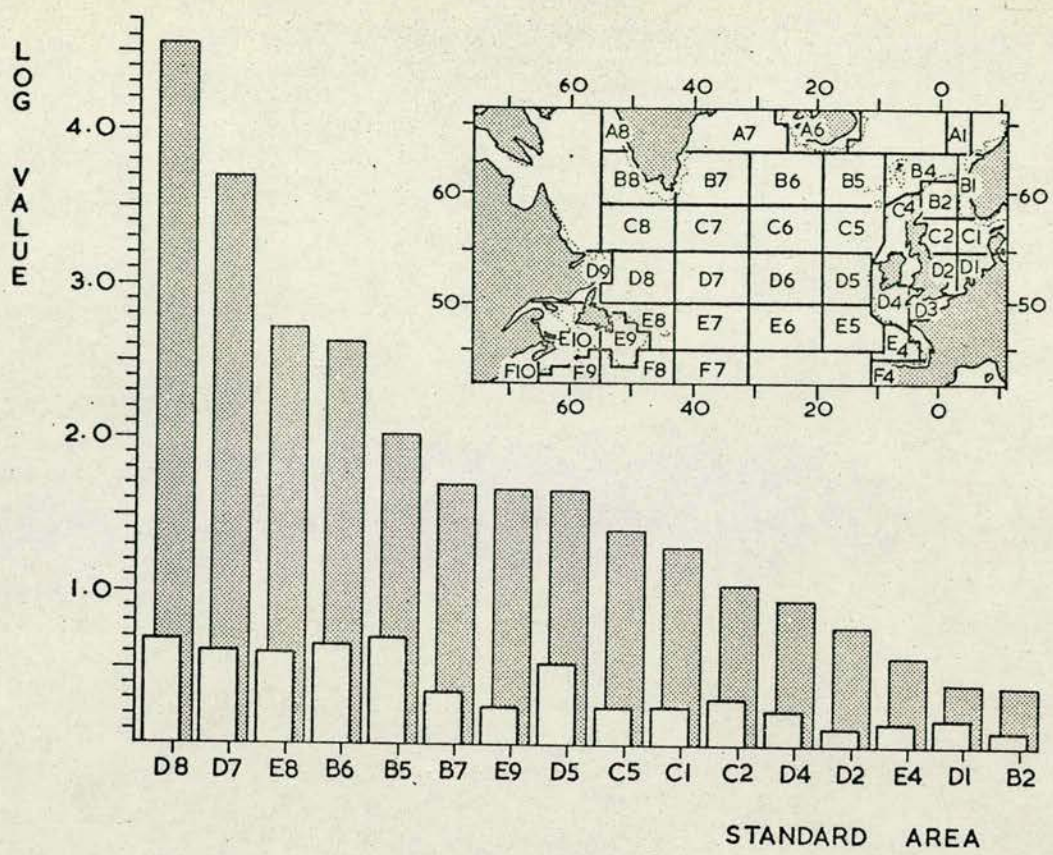

FIGURE 19 -- Average densities of hyperiids in the surface waters of the selected standard areas (compare letter-number codes with inset) during 1962-5, at night (shaded) and during the day (white).

ratios, below), variations occurred. Thus, from May to September the ratio[1] of night/day densities was higher than in other months of the year:

Month:	Jan	Feb	Mar	Apr	May	Jun	Jul	Aug	Sep	Oct	Nov	Dec
Ratio[1]:	3.5	4.5	2.4	4.0	7.1	8.7	5.7	9.4	5.9	3.3	4.0	5.0

[1]For calculation of this ratio, log values were first changed to arithmetic numbers; that is, each 10log(x+1) was divided by ten, converted to antilogarith and reduced by one.

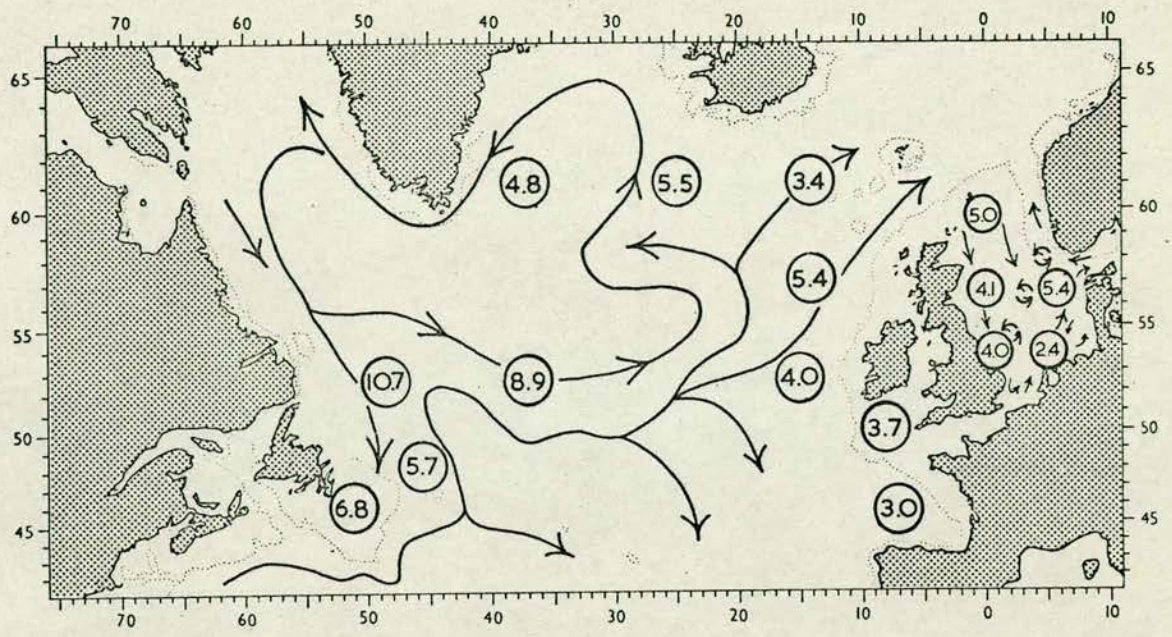

FIGURE 20 -- Geographical distribution of night/day ratios of the density of hyperiids in surface waters during 1962-5. Ratios, calculated from antilogs (-1) of mean "log values" representing numbers of animals over selected standard areas, are here superimposed (at the approximate centres of these areas) on the generalized diagram of surface circulation given earlier in Fig. 1.

Furthermore the ratio was also relatively higher in areas to the north-east and east of Newfoundland (D7, D8 and E9, Fig. 20), where water of the Labrador Current and subarctic gyre are approached by the Gulf Stream current and its major meander northward into the western Atlantic basin (cf. Fig. 1). As a consequence of the diurnal effect, therefore, the average abundance in near-surface waters of this region (as compared with other areas) might be over-estimated at night, especially during the summer.

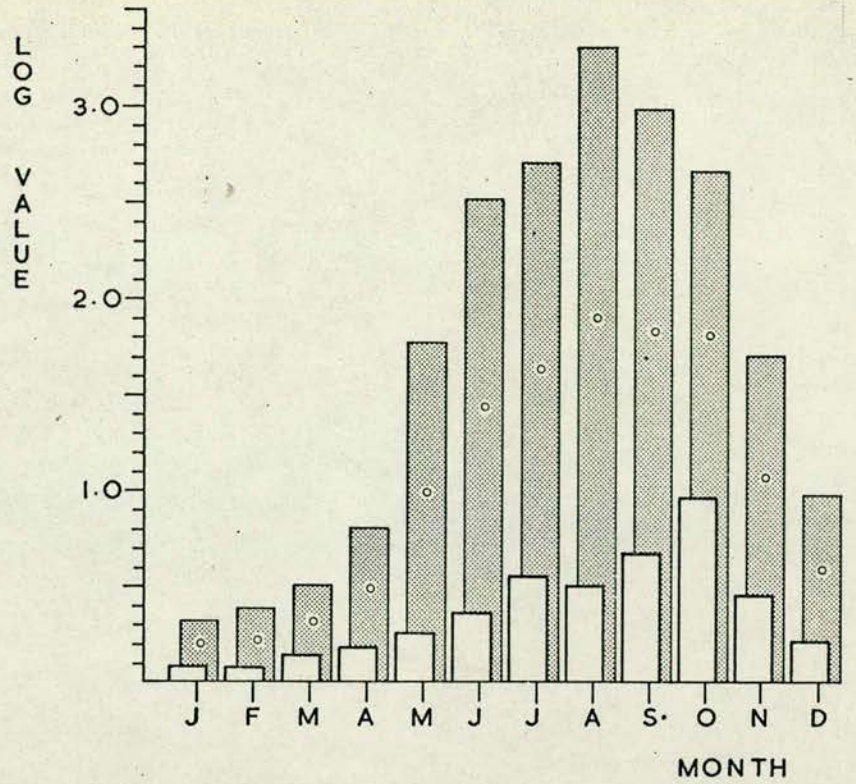

FIGURE 21 -- Average monthly densities of hyperiids in surface waters of the selected standard areas during 1962-5 from samples taken at night (shaded), by day (white) and from all samples (circle).

The monthly means in Fig. 21 show a clear seasonal cycle in the abundance of hyperiids in surface waters. Though numbers were on average highest in August, September and October and lowest in January (circles), the seasonal peak of animals sampled by night (shaded) was in August while that for those taken by day (white) occurred in October.

The seasonal cycle of hyperiid abundance varied in amplitude (M x A, Table 7) between areas. As shown by sampling at night (months, Table 8), the seasonal change was

TABLE 8 -- Analyses of variance to show, for each selected standard area, the effects of months (df=11) and years (df=3) on the density of hyperiids in the surface waters at night. Upper and lower numbers for each area are mean sum of squares and percentage mean sum of squares, respectively. Level of significance implied (but not verified) : *=5%, **=1%.

	MONTHS												YEARS			ERROR
	9	8	7	6	5	4	3	2	1							
B			1828.5** 88	3081.9** 68	1682.8** 54			76.5* 68					3.1 3	32.0 29		
C					943.3** 24			93.3 20	487.3* 31				312.3** 68	53.0 12	870.3* 55	211.7 14
D		4353.0** 77	3806.8** 64		902.5* 17	212.1 14		215.0* 28	49.1 52				470.3** 60	95.0 12	2.8 3	43.1 45
E	439.5 44	766.1 50			•	76.1 41										
B			62.7 3	662.3 15	1023.3* 32			3.1 3					180.3 9	759.4 17	436.7 14	
C					2676.8** 69			312.3** 68	870.3* 55				288.7 7			
D		534.3 10	1560.0 26		4010.3** 75	980.7* 67		470.3** 60	2.8 3				625.3 10	743.2 13	425.5 8	276.4 19
E	118.2 12	101.7 7				43.7 24										64.0 35
B			180.3 9	759.4 17	436.7 14			32.0 29								
C					288.7 7			53.0 12	211.7 14							
D		743.2 13	625.3 10		425.5 8	276.4 19		95.0 12	43.1 45							
E	433.3 44	667.4 43				64.0 35										

of greater significance in subarctic and northern (cooler) North Atlantic Drift waters than in waters of the southern (warmer) Drift, the Gulf Stream current, or the neritic regions. The cycle varied furthermore in pattern. Whereas a single maximum was characteristic of hyperiid abundance in

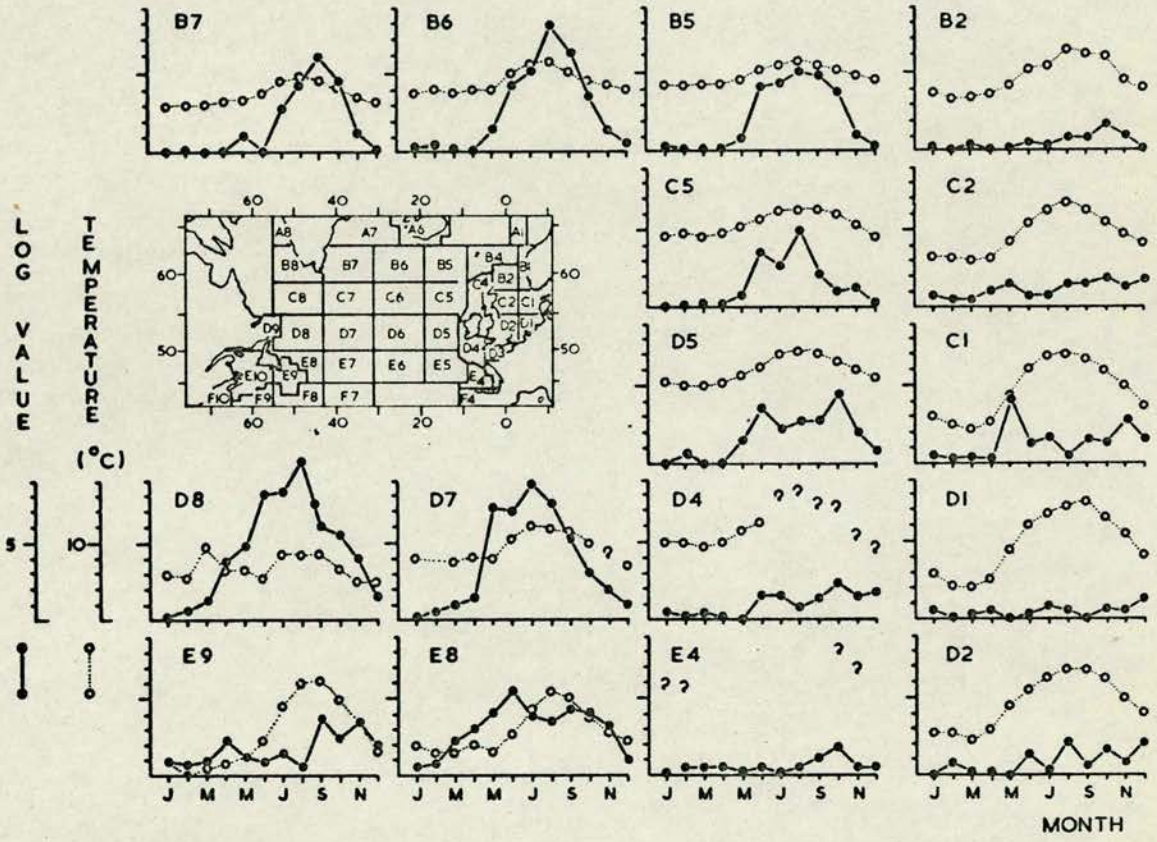

FIGURE 22 -- Monthly densities of hyperiids in the surface water at night, for each selected standard area during 1962-5 (closed circles). Sea-surface temperatures from the same statistical squares and months as plankton was sampled at night during 1962-5 (open circles), taken where available from data of the British Meteorological Office and the Danish Meterorological Institute (1964). Average temperatures marked "?" are perhaps less reliable because they are based on data from fewer than four years.

TABLE 9 -- Product moment coefficients of correlation (x 10) and rounded off to the nearest whole number) arranged to show similarities, between standard areas, in the seasonal fluctuations of density of hyperiids collected at night. Bold type denotes coefficients greater than 0.4; areas on lower right fit poorly into the pattern.

	E8	**7**	**8**	**6**	**6**	**7**	**6**	**7**	**5**	4	3	4	4	-1	**5**	-4
	D7	**9**	**9**	**9**	**8**	**5**	**6**	2	0	2	1	-1		1	4	-2
	D8	**9**	**9**	**9**	**6**	**7**	4	2	3	2	0			3	2	-1
	C5	**9**	**9**	**5**	**7**	3	1	3	0	-1				-5	2	-1
	B6	**10**	**8**	**8**	**5**	4	4	2	1					4	0	-1
Oceanic	B5	**8**	**9**	**6**	**5**	**6**	2	2						4	0	-1
	B7	**7**	**7**	**7**	**5**	**5**	**5**							3	3	-2
	D5	**8**	**7**	**8**	**5**	4								**5**	3	-1
Warm	B2	**8**	**7**	**5**	**5**									4	1	-1
	E4	**6**	**6**	4										4	-1	-1
Neritic	D4	**5**	**6**											**6**	1	**5**
	C2	**7**												3	-2	2
Cold	E9													-1	4	0
Neritic	D2													-2	4	
	C1													-2		
	D1															

subarctic water, peaks in Drift and neritic waters were of variable number and of lesser magnitude (Fig. 22, closed circles). The areal distribution of abundance would consequently vary depending on the season of observation.

Not surprisingly, the form of the seasonal cycle showed greater similarity in adjacent areas than between

widely separated ones. The matrix of correlation coefficients in Table 9 illustrates this geographical pattern and indicates that those areas with the most striking monthly fluctuations in hyperiid numbers (cf. Table 8, Months) also show the most similarity in the shape of the seasonal change.

Areas on the diagonal in Table 9, ranked according to the interrelation of their seasonal cycles of hyperiid numbers, appear to fall into climatological subgroups. For example, there is a basic but overlapping division into oceanic and neritic regions, the boundary falling approximately between areas D5 and B2 (Table 9). Further the oceanic group may be subdivided into western (E8, D7 and D8), northeastern (C5) and northern (B6, B5 and B7) regions influenced predominantly by subarctic and northern North Atlantic Drift water, and a south-eastern area (D5) in the southern part of the North Atlantic Drift. Similarly, areas of the neritic group might be separated geographically into those of the Drift current (B2, E4 and D4), the northern North Sea (C2), and the Labrador Current (E9).

Only three of the areas (D2, C1 and D1) could not be fitted into the basic matrix groupings in Table 9. The correlation coefficients in these areas (all in the central and southern North Sea) were low and suggest that the seasonal cycles in these areas were unrelated to those in all other areas of this study. On the other hand, this

type of evidence may be a reflection of the very low numbers of hyperiids sampled in the central and southern North Sea which are perhaps inadequate, in this case, for a valid test of correlation.

Examination of Fig. 22 (closed circles) indicates that hyperiids of subarctic and cooler Drift waters in the north-east (C5) and north (B6, B5 and B7) tend to increase in abundance about three months after those in the west (E8, D7 and D8). The major part of this delay does not seem to be a simple temperature effect as the surface water was not colder in certain of those areas where hyperiids appeared late (compare, for example, winter-spring temperatures in B6 and B5 with those in D8 and E8). Nor, apparently was the time of summer increase in temperature consistently related to the growth of abundance. In areas D7 and E8, for instance, the growth of hyperiid numbers preceded the seasonal rise in temperature.

The length of day is shorter at higher latitudes during the winter-spring months concerned. This might contribute to the delayed appearance of hyperiids in the north. If this were the case, hyperiid increases in the north-east (areas C5 and D5) would presumably be deferred less than those further north. This was only partly true, however, as the increase was relatively late in the north-east (see Fig. 22, closed circles) and, moreover, the seasonal fluctuation, in area D5 particularly, compared more closely with changes further north than with those in the west (cf. Table9).

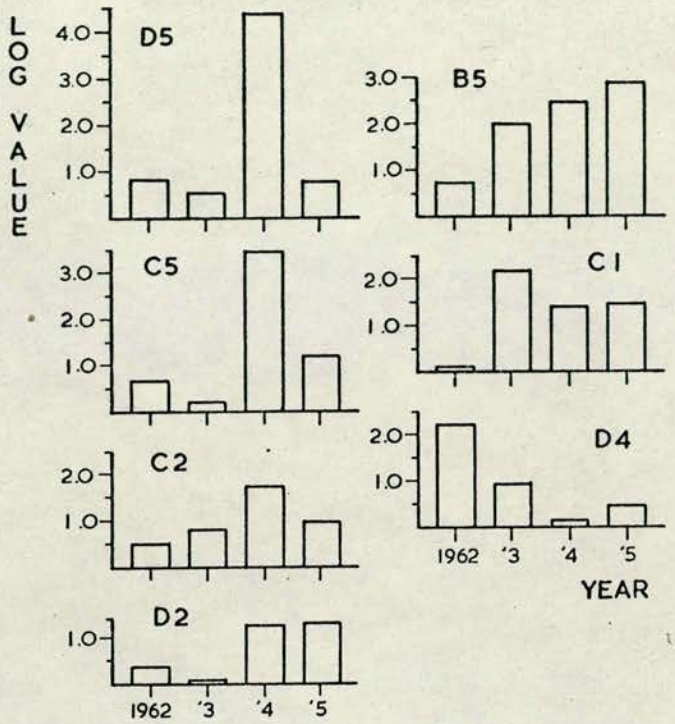

FIGURE 23 -- Annual densities of hyperiids in the surface water at night, for those selected standard areas where yearly variation from 1962 to 1965 was possibly significant (as indicated in Table 8).

This apparent anomaly may have been produced as a result of another factor, high summer temperature in the east. The possibility of suppressed breeding (and hence of delayed increase in numbers) at upper levels of temperature tolerance will be discussed later (section G3.3).

In most of the 16 areas selected for examination of abundance, hyperiid numbers varied little between the four

years, 1962-5 (Years, Table 8). Mean log values, in chronological order, were 1.33, 1.57, 2.13 and 1.84. Those few regions in which abundance did change noticeably, lay in the North Sea (C1, C2 and D2) and in the Atlantic immediately west of the British Isles (B5, C5, D5 and D4; astrices, years, Table 8); the annual fluctuations in these areas are shown in Fig. 23. Within the North Atlantic Drift current (D5 and C5) and in the north-western part of the NorthSea (C2), animals were more abundant in 1964 than in other years. Perhaps during this year beneficial conditions were shared by these regions. No similar annual variation was shown by specimens in other areas (Fig. 23).

F2 Taxonomic composition of hyperiids

F2.1 Genera

Nineteen genera were identified from the material examined (Table 10). Sixteen of these came from areas within the influence of the Gulf Stream current and southern parts of the North Atlantic Drift; three were taken mainly in subarctic water but also occurred in the North Sea. On this basis and for lack of better terms the larger number of genera (16) were referred to as "warm-water" while the fewer, as "cold-water". One genus, Hyperia, is treated as two, however, because subgenus Parahyperia is a warm-water taxon whereas subgenus Hyperia is cold-water in nature.

TABLE 10 -- Systematic list[1] of hyperiids found in the present survey.

HYPERIIDEA GAMMARIODEA

TRIBUS DERIVATA

Family Scinidae
- Genus Scina

Family Vibiliidae
- Genus Vibilia

HYPERIIDEA GENUINA

TRIBUS RECTICORNIA

Family Paraphronimidae
- Genus Paraphronima

TRIBUS FILICORNIA

Family Hyperiidae
- Genus Hyperoche
- Genus Hyperia
  - Subgenus Hyperia
  - Subgenus Parahyperia
- Genus Parathemisto
  - Parathemisto abyssorum
  - P. gaudichaudii
  - P. gracilipes
  - P. libellula
- Genus Phronimopsis

Family Phronimidae
- Genus Phronima
- Genus Phronimella

Family Anchylomeridae
- Genus Phrosina
- Genus Primno

TRIBUS CURVICORNIA

Family Phronoidae
- Genus Eupronoe"
- Genus Parapronoe"
- Genus Paralycaea
- Genus Lycaea

Family Brachyscelidae
- Genus Brachyscelus
- Genus Thamneus

Family Oxycephalidae
- Genus Rhabdosoma

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[1]The classification to family followed here is that used by Stephensen (1925) in his systematic list of the Hyperiidea.

TABLE 11 -- Occurrences of hyperiids rare in the present survey, giving for each taxon: the month, year, position, standard area and number of specimens identified.

MONTH	YEAR	POSITION °N	POSITION °W	AREA	NO.
Scina					
Jun	65	41.5	46.0	F8	1
Vibilia					
Apr	65	46.5	6.0	E4	1
Aug	65	51.5	14.0	D5	1
Paraphronima					
Oct	64	44.5	44.0	F8	2
Hyperoche					
Aug	62	61.5	28.0	B6	1
Aug	62	60.5	26.0	B6	1
Jul	63	44.5	64.0	E10	2
Jul	63	43.5	66.0	F10	3
Sep	63	53.5	50.0	D8	1
		°N	°E		
Dec	63	54.5	2.0	D2	1
Jan	64	57.5	4.0	C1	1
Jun	64	54.5	2.0	D2	2
		°N	°W		
Jul	64	61.5	30.0	B6	1
Jul	64	56.5	2.0	C2	1
Aug	64	57.5	36.0	C7	1
Jan	65	45.5	54.0	E9	1
May	65	41.5	46.0	F8	1
		°N	°E		
May	65	54.5	6.0	D1	1
		°N	°W		
Nov	65	54.5	50.0	D8	1
Nov	66	56.5	2.0	C2	1
Hyperia (Hyperia)					
Jul	62	43.5	66.0	F10	1
Sep	62	44.5	62.0	E10	1
Oct	62	43.5	64.0	E10	1
Jul	63	44.5	64.0	E10	3
Apr	64	61.5	24.0	B6	1

MONTH	YEAR	POSITION °N	POSITION °W	AREA	NO.
Hyperia (Parahyperia)					
Sep	63	44.5	42.0	F7	1
Sep	63	44.5	46.0	F8	1
Sep	64	43.5	46.0	F8	1
Oct	64	44.5	44.0	F8	1
Aug	65	42.5	58.0	F8	1
Sep	65	43.5	44.0	F8	1
Parathemisto abyssorum					
Jul	63	52.5	52.0	D8	2
Jul	63	53.5	53.5	D8	1
Aug	63	52.5	54.0	D9	1
Oct	63	53.5	52.0	D8	1
Sep	64	60.5	8.0	B4	3
Sep	65	61.5	2.0	B4	1
Parathemisto libellula					
Jul	63	53.5	52.0	D8	2
Jul	63	53.5	52.0	D8	1
Jul	63	52.5	52.0	D8	3
Jul	63	52.5	54.0	D9	2
Jul	63	52.5	56.0	D9	1
Aug	64	54.5	52.0	D8	1
Phronimopsis					
Sep	65	43.5	42.0	F7	1
Phronima					
Jan	62	47.5	12.0	E5	1
Apr	62	47.5	12.0	E5	1
May	62	48.5	12.0	E5	3
Mar	65	48.5	6.0	D4	1
Apr	65	50.5	44.0	D8	1
Apr	65	45.5	8.0	E4	2
Sep	65	43.5	42.0	F7	1
Phronimella					
Sep	63	44.5	46.0	F8	1
Nov	66	44.5	44.0	F8	1
Phrosina					
Jan	65	43.5	44.0	F8	1
Aug	65	43.5	42.0	F7	1
Sep	65	42.5	62.0	F9	1
Nov	65	43.5	44.0	F8	2
Nov	66	44.5	44.0	F8	1

Continued next page.

TABLE 11 -- Continued.

MONTH	YEAR	POSITION °N	POSITION °W	AREA	NO.
Primno					
May	62	47.5	12.0	E5	1
Nov	63	44.5	46.0	F8	1
Nov	63	44.5	44.0	F8	1
Sep	64	43.5	46.0	F8	1
May	65	42.5	44.0	F8	1
Aug	65	42.5	46.0	F8	2
Jul	66	46.5	8.0	E4	1
Eupronoë					
Nov	63	44.5	44.0	F8	1
Aug	65	42.5	46.0	F8	1
Parapronoë					
Jun	65	45.5	8.0	E4	1
Paralycaea					
May	65	45.5	16.0	E5	1
Lycaea					
Aug	62	55.5	20.0	C6	1
Sep	65	42.5	60.0	F9	1
Brachyscelus					
May	62	47.5	12.0	E5	1
Mar	63	47.7	5.7	D4	1
Sep	63	47.5	10.0	E4	1
Oct	63	46.5	12.0	E5	1
Nov	63	47.5	12.0	E5	1
Nov	63	46.5	14.0	E5	1
Feb	64	47.3	6.3	E4	1
Thamneus					
Sep	63	44.5	42.0	F7	1
Oct	63	44.5	16.0	F5	1
Oct	63	47.5	10.0	E4	1
Nov	63	44.5	44.0	F8	1
Dec	64	43.5	44.0	F8	1
Rhabdosoma					
Sep	65	43.5	44.0	F8	1
Oct	66	44.5	46.0	F8	1
Apr	67	34.5	62.0	"G9"	1

All genera were rare but one. This exception, the cold-water genus Parathemisto had two species which seldom occurred and two which were abundant. The locations and times of collection of all the taxa excepting the two common species are given in Table 11.

Specimens of the "warm-water genera" were usually confined to the regions dominated by warm-water currents (Fig. 1) where they constituted from 1 to 43% of the total hyperiids examined from each area (Table 12; Fig. 24). On two occasions when individuals of these genera were

TABLE 12 -- Taxonomic composition of the hyperiids examined from each standard area. The composition expressed here as a percentage, depends for its validity mainly on the number of specimens examined (column next to last). Its relation to abundance is indicated by the log value of density at night (last column).

STANDARD AREA	GENERA				SPECIES OF PARATHEMISTO						
	"Warm-water"	Hyperia (Hyperia)	Hyperoche	Parathemisto[1]	P. libellula	P. abyssorum	P. gracilipes	P. gaudichaudii	"P. undetermined"[1]	Number of specimens examined	Mean density at night (log value)
	PERCENTAGE										
A1				100.0				14.6	85.5	124	1.29
A6				100.0				96.2	3.8	210	1.56
A7				100.0				83.8	16.2	37	2.89
A8				100.0				88.9	11.1	9	0.60
B1				100.0			9.4	14.1	76.5	64	0.33
B2				100.0			38.4	1.4	60.2	73	0.38
B4				100.0		1.1	0.9	69.0	29.0	351	0.93
B5				100.0				61.4	38.6	468	2.02
B6		0.2	0.5	99.3				41.6	57.7	607	2.62
B7				100.0				47.6	52.4	395	1.82
B8				100.0				3.4	96.6	59	0.83
C1			0.3	99.7			9.2	0.5	90.0	369	1.32
C2			0.5	99.5			14.8	2.5	82.2	406	1.05
C4				100.0			26.2	13.5	60.3	141	0.53
C5				100.0				61.0	39.0	387	1.71
C6	0.3			99.7				31.0	68.7	345	3.94
C7			0.3	99.7				28.3	71.4	389	2.63
C8				100.0				44.1	66.0	809	4.31
D1			1.8	98.2			30.4		67.8	56	0.40
D2			3.5	96.5			48.3	3.5	44.7	85	0.82
D3				100.0			60.0	30.0	10.0	10	0.16
D4	1.8			98.2			27.9	10.8	59.5	111	0.78
D5	1.1			98.9				49.5	49.4	91	1.70
D6				100.0				14.5	85.5	283	4.21
D7				100.0				22.0	78.0	318	4.65
D8	0.1		0.2	99.7	0.7	0.4		32.8	65.8	1018	4.59
D9				100.0	1.6	0.5		38.8	59.1	188	5.86

Continued next page.

[1]Percentages obtained by difference.

TABLE 12 -- Continued.

STANDARD AREA	GENERA				SPECIES OF PARATHEMISTO						
	"Warm-water"	Hyperia (Hyperia)	Hyperoche	Parathemisto[1]	P. libellula	P. abyssorum	P. gracilipes	P. gaudichaudii	"P. undetermined"[1]	Number of specimens examined	Mean density at night (log value)
	PERCENTAGE										
E4	15.5			84.5			53.5		31.0	58	0.52
E5	4.3			95.7			2.0	11.0	82.7	254	1.61
E8				100.0				29.7	70.3	239	2.90
E9			0.3	99.7			0.3	18.2	81.2	296	1.69
E10		4.1	1.6	94.3			1.6	27.8	64.9	122	1.57
F4				100.0			66.7		33.3	6	0.16
F5	16.7			83.3					83.3	6	
F7	26.7			73.4					73.4	15	1.11
F8	3.3		0.2	96.5			0.2	6.5	89.8	637	3.27
F9	42.9			57.1				57.1		7	1.77
F10		0.8	2.4	96.8			2.4	5.6	88.8	125	1.80

found in apparently cool water (Phronima in D8 and Lycaea in C6) they represented only 0.1 and 0.3%, respectively, of the total specimens investigated in these areas (Tables 11 and 12).

Whereas the "cold-water" genus Hyperoche and subgenus Hyperia were found scattered throughout the cold water regions of the North Atlantic, Hyperoche alone appeared also in the southern North Sea and in possibly

[1]Percentages obtained by difference.

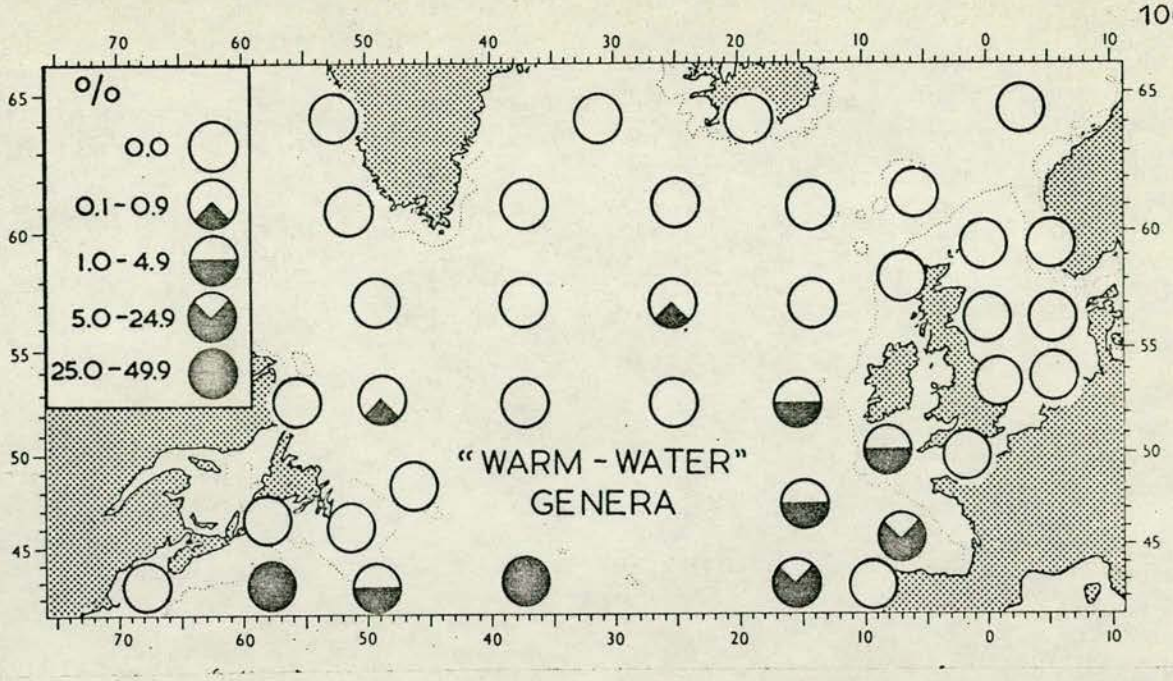

FIGURE 24 -- Percentage of hyperiids belonging to "warm-water genera" (for details see Table 12). Symbols drawn at the approximate centres of the standard areas represented.

warmer waters south-east of Newfoundland (Fig. 25). Each of these hyperiids was rare, contributing less than 5% of specimens in the areas where it was present (Table 12). In sharp contrast, Parathemisto accounted for 95 to 100% of the hyperiids examined in all but four areas where, incidently, warm-water genera were prevalent (cf. Figs. 24 and 26).

F2.2 Species of Parathemisto

Of the seven known species of Parathemisto, those four recognized to occur in the North Atlantic and North Sea were found in the material examined. Parathemisto libellula, was found in two standard areas, north and north-east of Newfoundland; while P. abyssorum, also found in these two

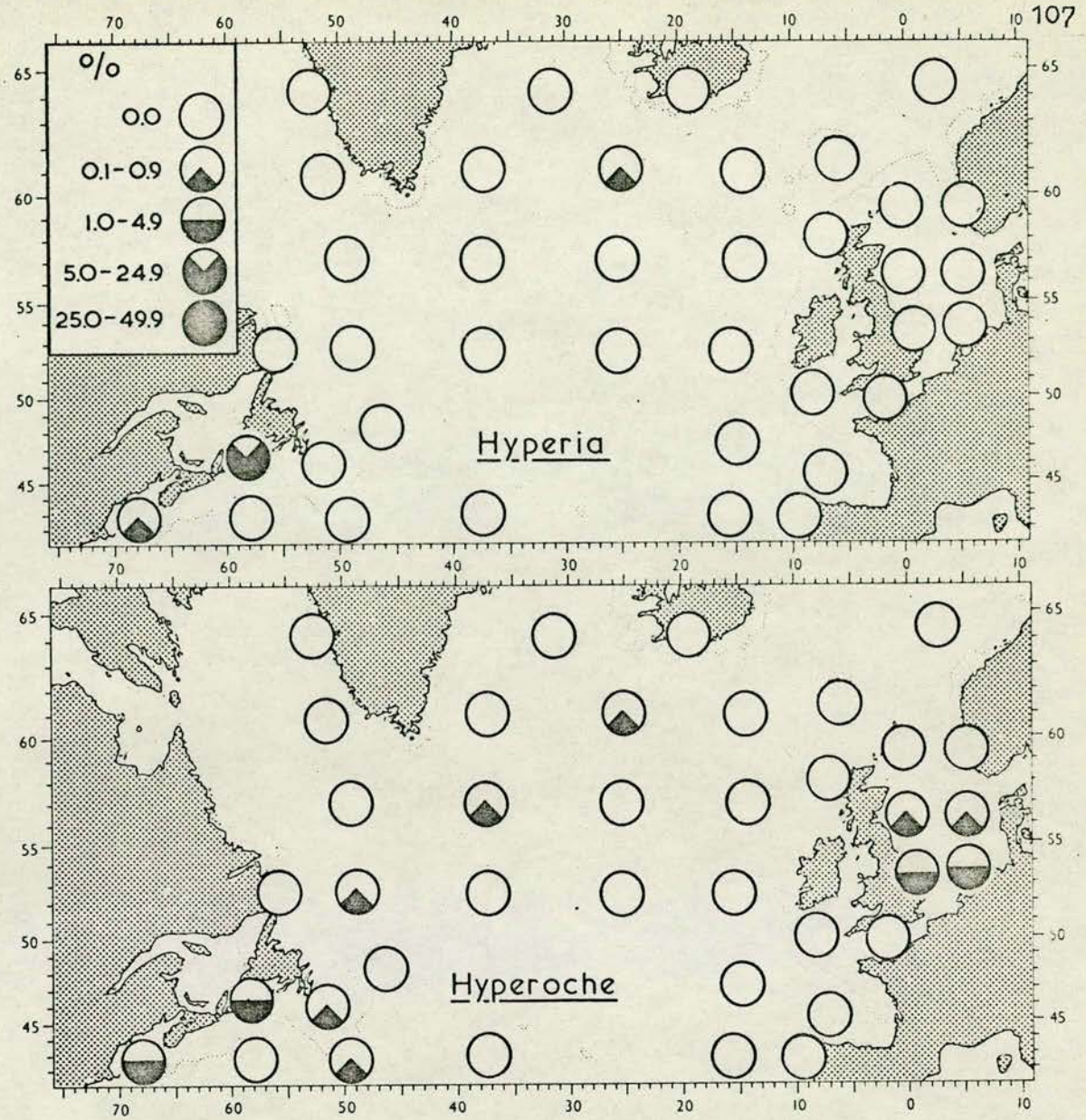

FIGURE 25 -- Percentages of hyperiids belonging to Hyperia (subgenus Hyperia only) and Hyperoche (for details see Table 12). Symbols drawn at the approximate centres of the standard areas represented.

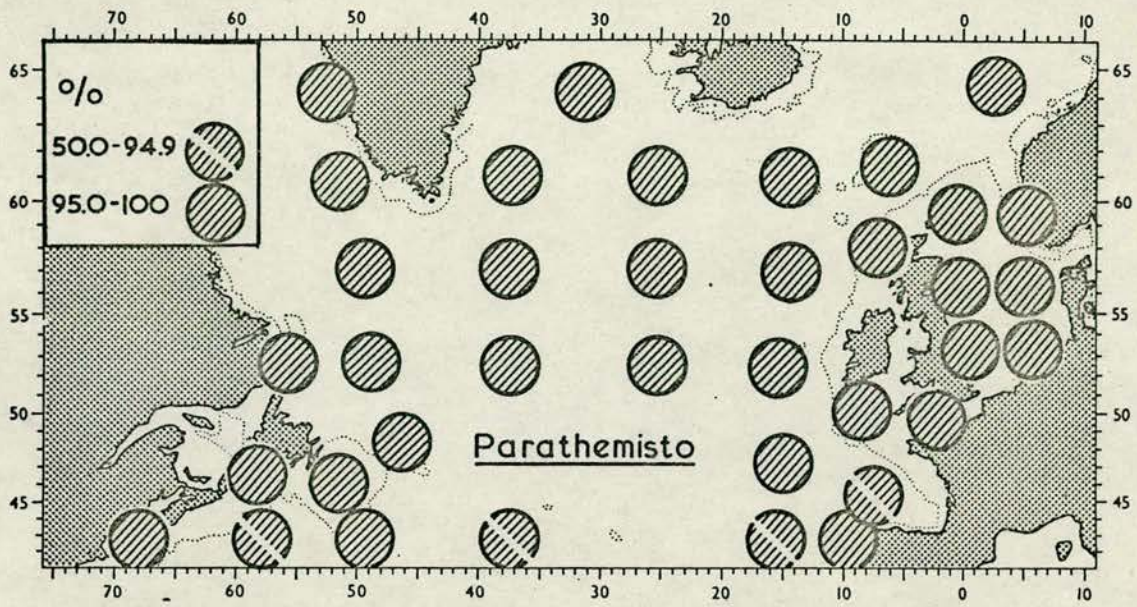

FIGURE 26 -- Percentages of hyperiids belonging to Parathemisto (for details see Table 12). Symbols drawn at the approximate centres of the standard areas represented.

areas, occurred as well in one area to the north of Scotland. Each contributed less than 2% to the total number of hyperiids collected in each area (Fig. 27).

The distributions of the common species, Parathemisto gracilipes and P. gaudichaudii, were complementary to one another with some degree of overlap. Out of 38 standard areas occupied by these two species, P. gracilipes was present in 16 and P. gaudichaudii in 33 (Table 12).

A large proportion of the Parathemisto material, however, could not be identified easily, much of it consisted of small specimens which were not examined for specific identity and a portion included larger ones (more than 3 mm)

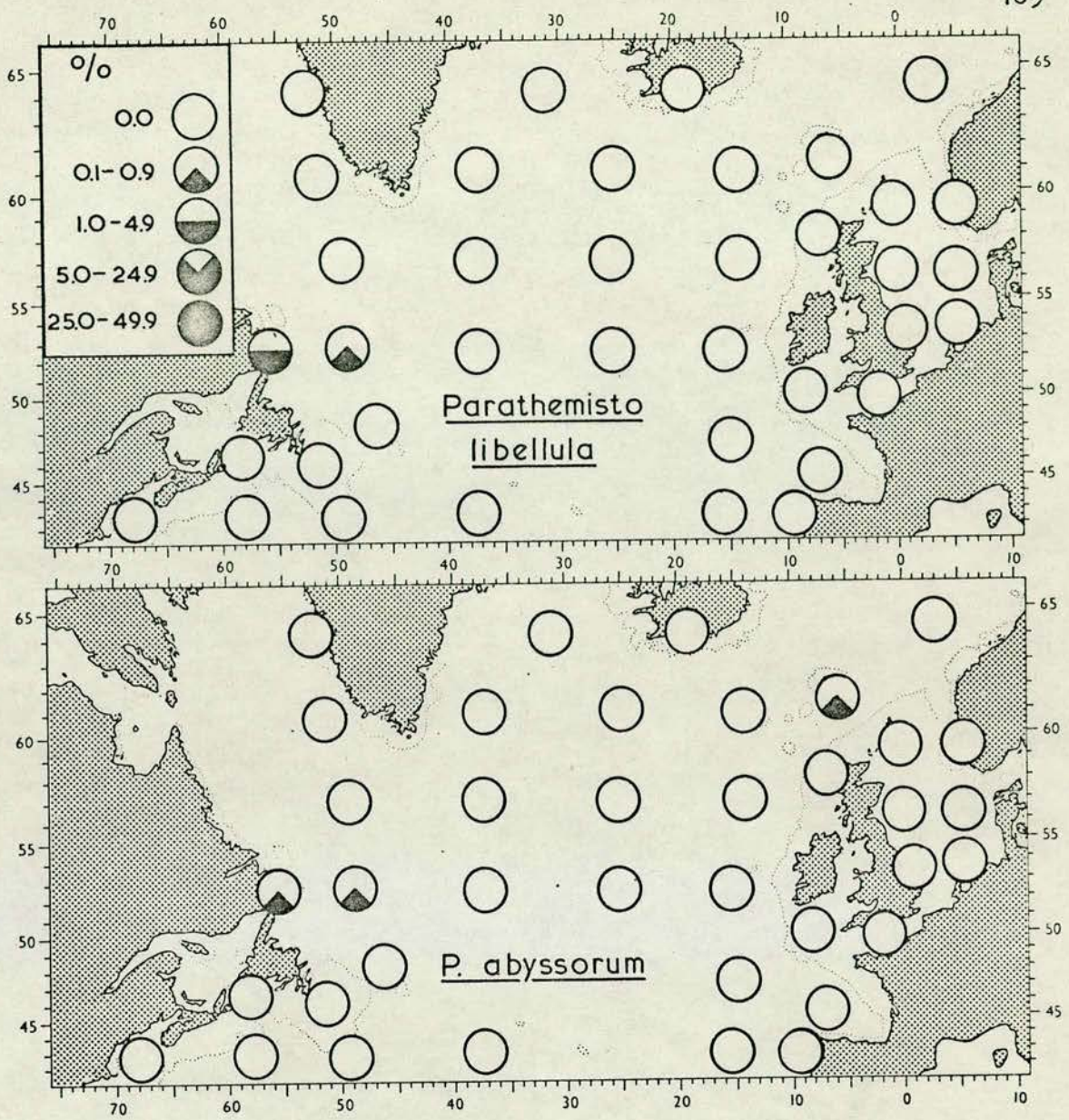

FIGURE 27 -- Percentages of hyperiids belonging to Parathemisto libellula and P. abyssorum (for details see Table 12). Symbols drawn at the approximate centres of the standard areas represented.

TABLE 13 -- Proportions[1] and densities of Parathemisto assumed to belong to P. gracilipes and P. gaudichaudii.[2] (See text for comments on biased data.)

AREA	PARATHEMISTO LOG VALUE	P. gracilipes PER CENT	P. gracilipes LOG VALUE	P. gaudichaudii PER CENT	P. gaudichaudii LOG VALUE
A1	1.29	0	0	100	1.29
A6	1.56	0	0	100	1.56
A7	2.89	0	0	100	2.89
A8	0.60	-	-	-	-
B1	0.33	40	0.13	60	0.20
B2	0.38	96	0.36	4	0.02
B4	0.93	1.3	0.01	97	0.92
B5	2.02	0	0	100	2.02
B6	2.60	0	0	100	2.60
B7	1.82	0	0	100	1.82
B8	0.83	0	0	100	0.83
C1	1.31	95	1.24	5.4	0.07
C2	1.04	86	0.89	14	0.15
C4	0.53	66	0.35	34	0.18
C5	1.71	0	0	100	1.71
C6	3.93	0	0	100	3.93
C7	2.62	0	0	100	2.62
C8	4.31	0	0	100	4.31
D1	0.39	100	0.39	0	0
D2	0.79	93	0.73	7	0.06
D3	0.16	67	0.11	33	0.05
D4	0.77	72	0.55	28	0.22
D5	1.68	0	0	100	1.68
D6	4.21	0	0	100	4.21
D7	4.65	0	0	100	4.65
D8	4.58	0	0	97	4.44
D9	5.86	0	0	93	5.86
E4	0.44	100	0.44	0	0
E5	1.54	17	0.26	83	1.28
E8	2.90	0	0	100	2.90
E9	1.68	2	0.03	98	1.65
E10	1.48	5.4	0.07	95	1.41
F4	0.16	100	0.16	0	0
F7	0.82	0	0	0	0
F8	3.16	3	0.10	97	3.06
F10	1.74	33	0.58	67	1.16

[1]Proportions based on material identifiable to species.

[2]Percentages up to 100% except at areas B4, D8 and D9 where Parathemisto abyssorum and P. libellula were represented (see Table 12 for details).

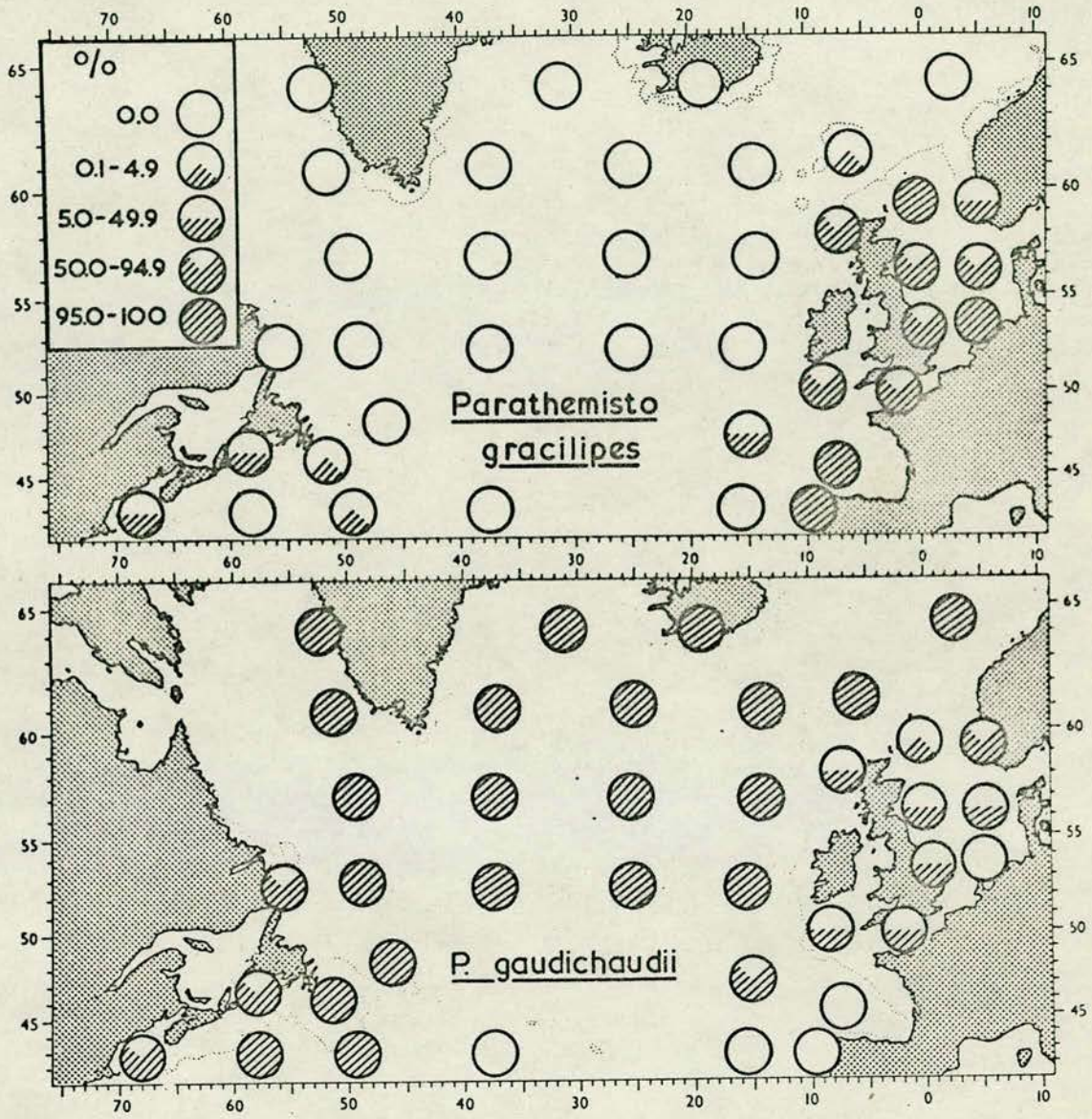

FIGURE 28 -- Percentage of Parathemisto belonging to P. gracilipes and P. gaudichaudii, assuming that undetermined members of the genus belong to either of these species in proportion to the ratio of specimens identifiable (for details see Table 13).

which were damaged or otherwise difficult to distinguish between the two species. It is assumed, therefore, that specimens of Parathemisto not determined to species belonged to either P. gracilipes or P. gaudichaudii in proportion to numbers of each species identified (Table 13,%). Figure 28 suggests the proportions of Parathemisto belonging to each of these species in each standard area.

F2.3 Morphological differentiation within Parathemisto gaudichaudii

From the evidence of the preceding section, virtually all hyperiids in waters of the subarctic system are assumed to belong to Parathemisto gaudichaudii. This holds even though many specimens cannot be definitely distinguished from P. gracilipes. On the basis of this belief, the following categories were defined to demonstrate degrees of morphological development within P.gaudichaudii:

Psp -- Animals belonging to the genus Parathemisto, measuring less than 3 mm in length, for which no attempt was made to assess the specific identity.

Pcg -- Animals measuring more than 3 mm in length which are assumed to belong to the species gaudichaudii although, at this stage, they cannot be separated morphologically from gracilipes.

Pbc -- Animals clearly belonging to the species gaudichaudii but intermediate in form between the

compressa and bispinosa forms.

Pb -- Animals clearly belonging to the bispinosa form of gaudichaudii.

Pc -- Animals clearly belonging to the compressa form of gaudichaudii.

In general terms the first two groups may be considered as being juvenile stages and the last two as the adults. The intermediate forms (Pbc) might be immature stages in the morphological development of the compressa and bispinosa forms or, in some cases, they may represent intermediate adults.

Figure 29, from a selection of night and day samples taken in subarctic areas (D8 and B6) and covering four seasonal periods and four years, gives the length frequency distributions of the five categories together with the summed distribution of the adult and near-adult forms (Pc+Pbc+Pb). In general it is apparent, as would be expected, that with increase in size, the animals become increasingly recognizable taxonomically.

Specimens of Parathemisto gaudichaudii recognized as male and female were generally large and almost invariably distinguishable as to the extreme forms, bispinosa and compressa (Pb and Pc). This sexual dimorphism was less strikingly demonstrated among those animals in the intermediate condition (Pbc). Table 14, resulting from examination of samples covering a range of diurnal, seasonal and

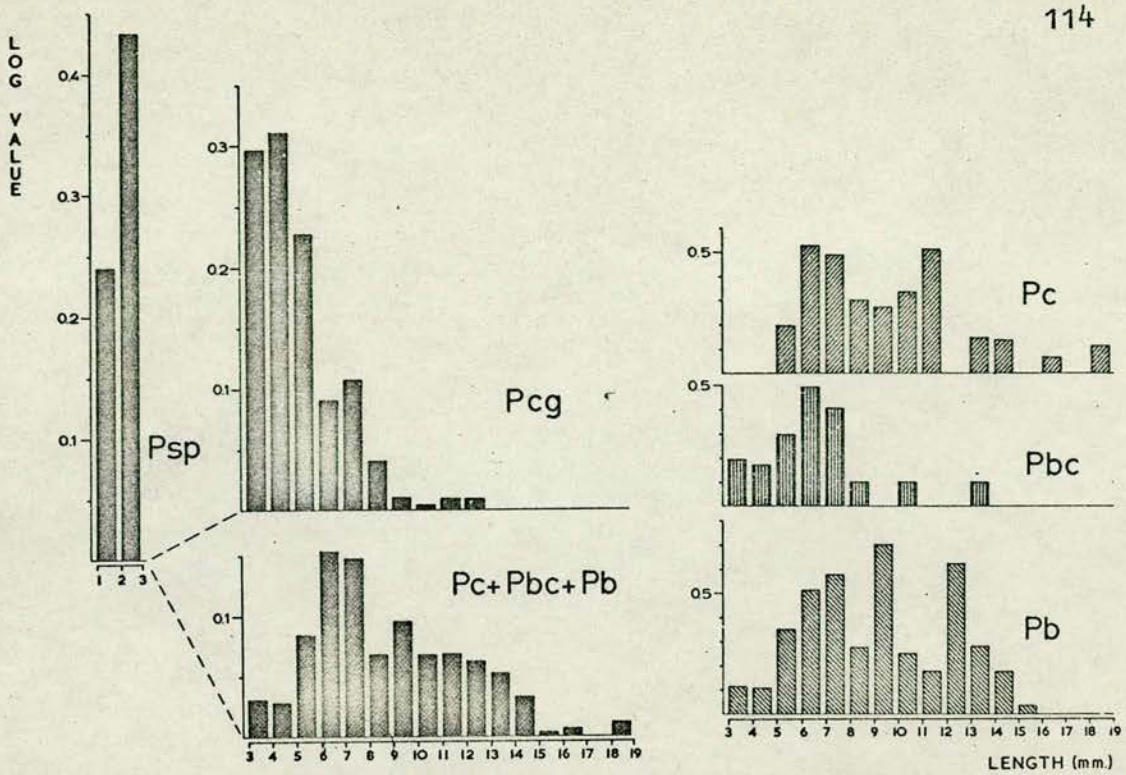

FIGURE 29 -- Length frequency distributions of specimens from regions occupied by Parathemisto gaudichaudii. Shown separately are distributions for:

Psp -- Parathemisto less than 3 mm in length and not identified to species.

Pcg -- Parathemisto more than 3 mm in length, assumed to be P. gaudichaudii but not distinguishable from P. gracilipes (definitely not P. abyssorum or P. libellula).

Pc+Pbc+Pb -- Parathemisto more than 3 mm and definitely P. gaudichaudii.

Pbc -- not clearly either bispinosa or compressa.

Pc -- form compressa.

Pb -- form bispinosa.

TABLE 14 -- Comparison of the proportions of specimens of Parathemisto gaudichaudii in four length ranges which have become differentiated morphologically to form (compressa or bispinosa) and sex. Data from exploratory examinations of a variety of CPR material (see section E3 for details).

Source of specimens	Length (mm) 0-3	3-7	7-12	12-∝	0-∝
	TOTAL NUMBERS OF SPECIMENS				
(B5)	29	38	40	33	
Gd	12	50	24	2	
Nb	446	203	58	44	
Sum	487	291	122	79	979
	NUMBERS DIFFERENTIATED TO FORM				
(B5)	0	26	37	33	
Gd	0	1	19	2	
Nb	0	22	55	44	
Sum	0	49	111	79	239
Percentage of total	0	17	91	100	24
	NUMBERS DIFFERENTIATED TO SEX				
(B5)	0	0	6	29	
Gd	0	0	9	2	
Nb	0	3	28	41	
Sum	0	3	43	72	118
Percentage of total	0	1	33	91	8
PROPORTION (x 100) OF NUMBERS DIFFERENTIATED: TO SEX / TO FORM					
	-	6	39	91	49

annual changes in subarctic waters occupied by P. gaudichaudii, indicates that about half (49%) of specimens clearly recognized to form possessed secondary characteristics for recognition of sex. This proportion, though it increased markedly with the size of specimen (bottom row, Table 14), shows the limited extent to which the percentage of determined specimens (Pb + Pc) may be used to indicate the sexual develpment of specimens in a sample and hence to suggest the reproductive maturity of a population.

F3 Geographical patterns of the common species

Table 13 (log value) gives values for the abundance of Parathemisto gracilipes and P. gaudichaudii calculated, from category estimates of samples collected at night, on the assumption that specimens of Parathemisto undetermined as to species belong to either of these two. Estimates for the density of undetermined specimens are provided in Table 15.

Figure 30 expresses, by an index of density, the year-round average distributions for Parathemisto gracilipes, for P. gaudichaudii and for those very numerous specimens of Parathemisto which could not be identified. These indices are antilogs of the log values estimated in Tables 13 and 15. Those based on less than nine months of sampling (Table 2) or fewer than ten specimens of analysis for species-composition (Table 12), were omitted from the

TABLE 15 -- Proportions and densities of Parathemisto "undetermined" as to species.

STANDARD AREA	PARATHEMISTO LOG VALUE	"PARATHEMISTO PER CENT	UNDETERMINED" LOG VALUE
A1	1.29	86	1.11
A6	1.56	4	0.06
A7	2.89	16	0.46
A8	0.60	-	-
B1	0.33	77	0.26
B2	0.38	60	0.23
B4	0.93	29	0.27
B5	2.02	39	0.79
B6	2.60	58	1.51
B7	1.82	52	0.95
B8	0.83	97	0.81
C1	1.31	90	1.18
C2	1.04	81	0.84
C4	0.53	60	0.32
C5	1.71	39	0.67
C6	3.93	69	2.71
C7	2.62	72	1.89
C8	4.31	66	2.84
D1	0.39	69	0.27
D2	0.79	46	0.36
D3	0.16	10	0.02
D4	0.77	61	0.47
D5	1.68	50	0.84
D6	4.21	86	3.62
D7	4.65	78	3.63
D8	4.58	67	3.14
D9	5.86	59	3.46
E4	0.44	36	0.16
E5	1.54	87	1.34
E8	2.90	70	2.03
E9	1.68	81	1.36
E10	1.48	69	1.02
F4	0.16	33	0.05
F5	-	-	-
F7	0.82	100	0.82
F8	3.16	93	2.94
F9	1.01	-	-
F10	1.74	92	1.60

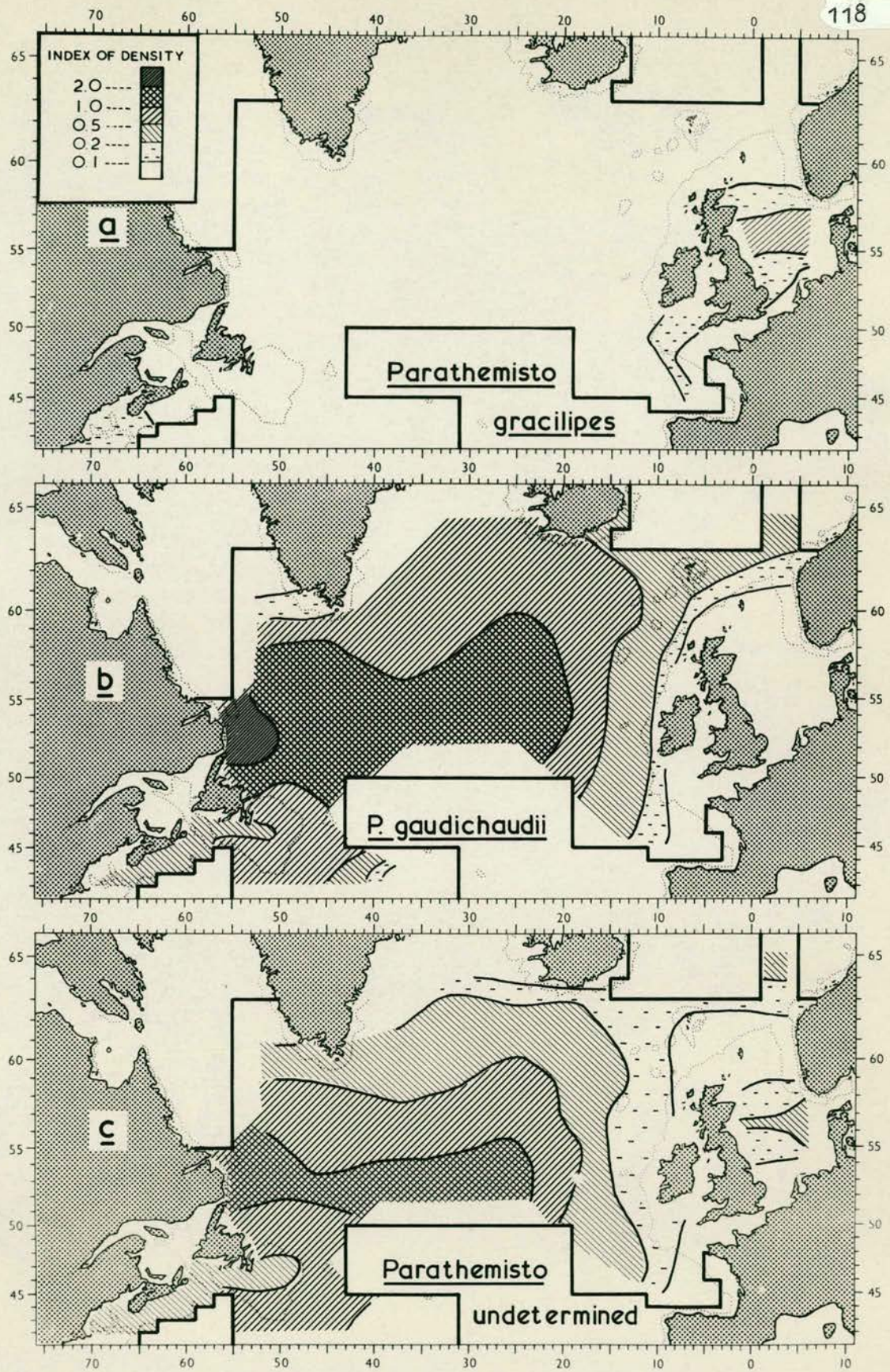

FIGURE 30 -- Legend at foot of following page.

figure. Off the Labrador coast of Canada where ice prevents adequate sampling in winter, the results may have been biased by a predominance of samples taken in summer. Nevertheless, though perhaps not representative in this particular region, the densities indicated in Fig. 30 give a reasonable approximation for the overall distribution of abundance.

Figure 31 shows the distribution of undetermined Parathemisto sampled at night during the months of August and September. Superimposed on this description are symbols indicating which of the two common species were present in each area; where both species occurred the larger symbol marks that most frequent. Since during these months all areas were similarly well sampled (Fig. 3b), the pattern shown in Fig. 31 might be considered to give a fairly unbiased representation.

Nevertheless, for several reasons the densities indicated in this figure (Fig. 31) might be considered somewhat too high, especially in the subarctic regions. As was shown earlier, numbers at night and during the

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FIGURE 30 -- Year-round average distributions of density for: a, Parathemisto gracilipes b, P. gaudichaudii and c, Parathemisto undetermined (mainly young), estimated with certain assumptions regarding the identity of specimens not determined and without regard for certain sampling bias (see text and Tables 13 and 15 for details).

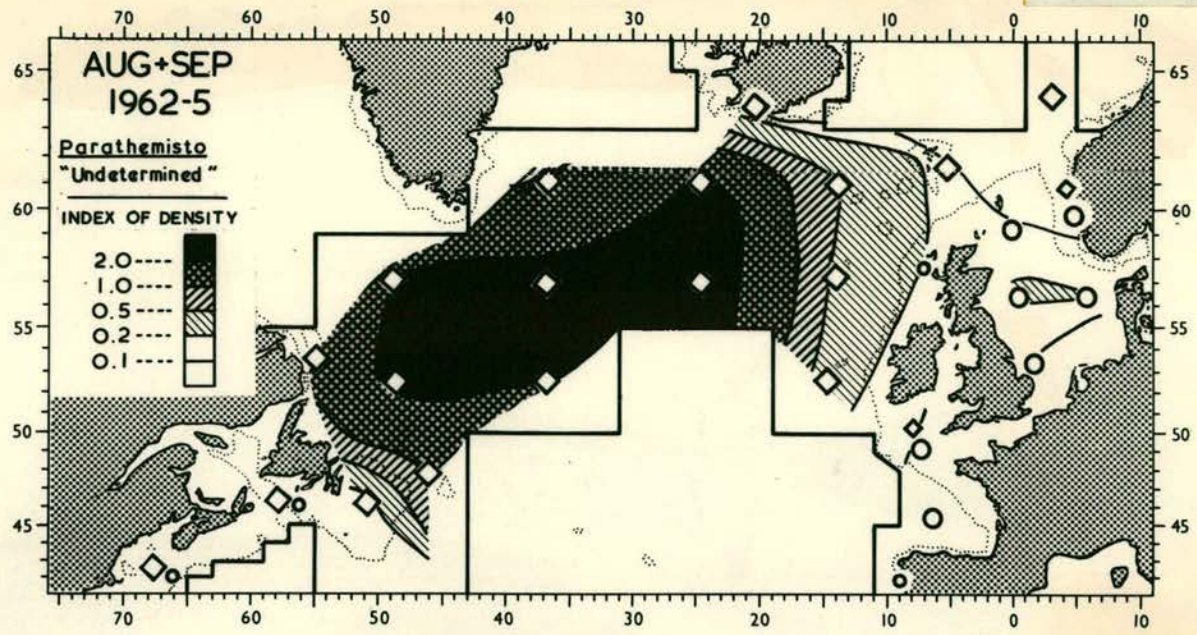


FIGURE 31 -- August-September distribution of density of undetermined, mainly young, Parathemisto in surface waters of the North Atlantic and North Sea during the nights of August and September, 1962-5. Parathemisto gaudichaudii (diamonds) or P. gracilipes (circles) was positively identified in more (large symbols) or less (small symbols) than one quarter of the months sampled.

warm season were consistently higher than at other times. Should this increase have been evenly distributed, the horizontal gradients shown would remain representative. However, since the night collections taken in certain subarctic areas off Newfoundland contained greater quantities than elsewhere in relation to day samples, geographical differences might have been exaggerated. Furthermore, whereas in southern North Atlantic Drift and

neritic regions hyperiids exhibited multiple (and sometimes indistinct) peaks of abundance throughout the year, those in subarctic and northern Drift waters demonstrated a single maximum in the August-September period represented in Fig. 31. These effects tend to emphasize unduly, the greater abundance present in subarctic water.

Figure 32(upper) shows, on statistical squares (1° latitude by 2° longitude) of the North Sea and vicinity, the distribution of those Parathemisto undetermined as to species (Psp and Pcg). Data for five years (1962-6) has been averaged for winter-spring and summer-autumn periods, each represented by three months of sampling. Densities and taxonomic composition for this presentation are not from category estimates or selected samples but are based on the examination and enumeration of all animals. Unlike the index of density in Figs. 30 and 31, therefore, the values used in Fig. 32(upper) are not antilogs but are actual counts expressed as the number of specimens per sample. The lower charts in Fig. 32 are presented to indicate that the proportion of night/day samples did not bias the results.

F3.1 Distribution of Parathemisto gracilipes

The greatest concentrations of Parathemisto gracilipes (index of density, 0.2 - 0.5) occurred mainly in the North Sea between 55 and 57° N (Fig. 30a). Lesser amounts were found in other parts of the North Sea and in the North Atlantic, particularly where warm water was likely to have approached the coasts of Europe and America (cf. Fig. 1).

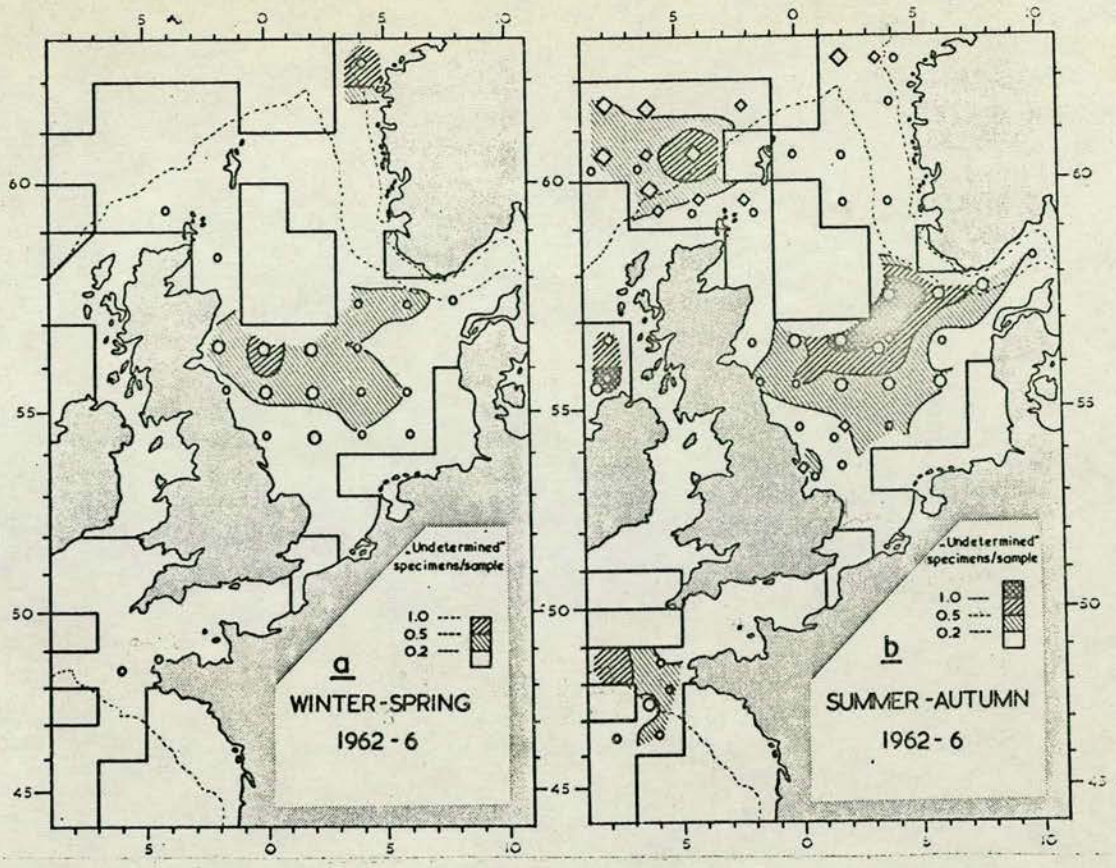
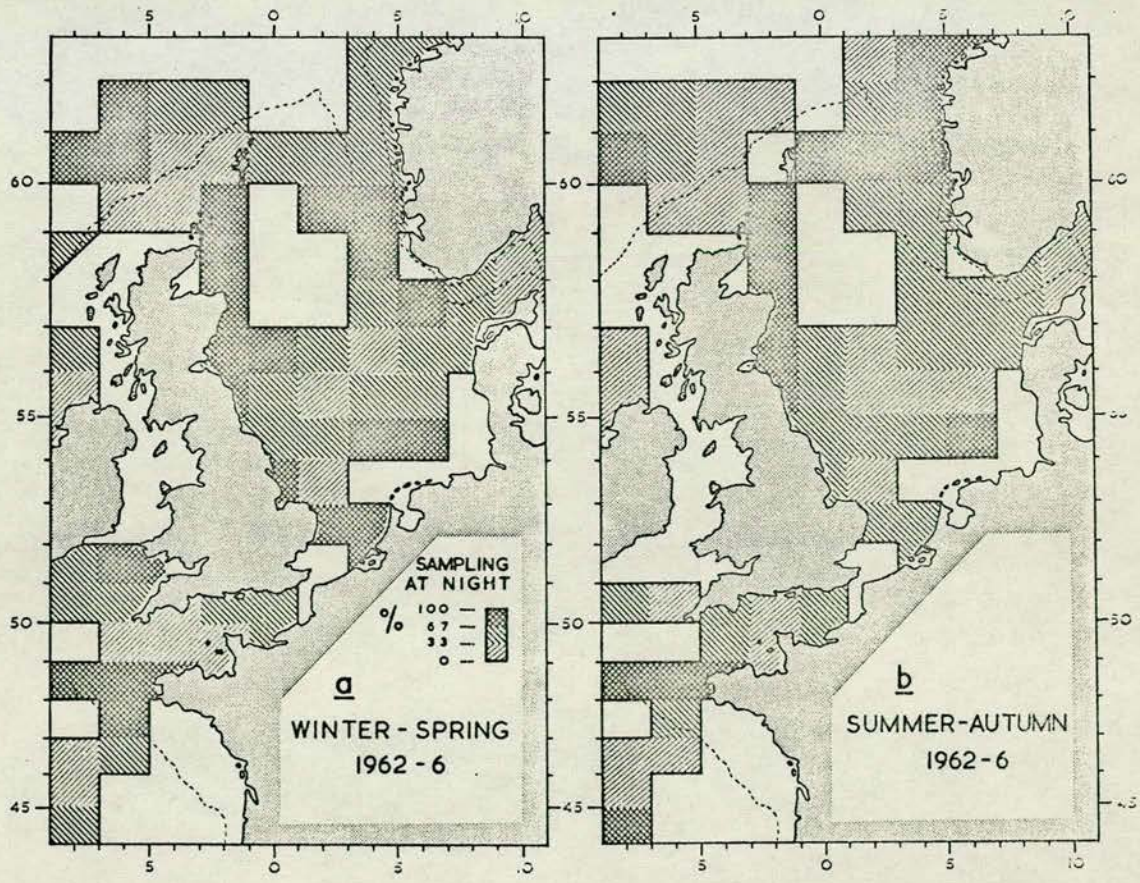


FIGURE 32 -- Legend at foot of following page.



As indicated earlier, undetermined specimens occurring in the presence of predominantly Parathemisto gracilipes may include, as well as many young, some adults or near-adults of this smaller species. The distribution of "Parathemisto undetermined" in the North Sea (Fig. 30c), therefore, though undoubtedly representing P. gracilipes in the main, does not necessarily give a good index of the extent of breeding.

Figure 31 shows, for undetermined Parathemisto in the North Sea during August and September, a somewhat restricted geographical distribution of abundance. As densities here were not especially high during these months (closed circles, Fig. 22), this pattern for P. gracilipes would appear to be quite plausible. At this time the species was present not only in the North Sea (circles, Fig. 31), but also off the European coast south of the British Isles and, at a lesser frequency, off the coast of America south of Newfoundland.

During the months of winter and spring which were examined for hyperiids in the North Sea, Parathemisto

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FIGURE 32 -- Distributions in the North Sea and vicinity, 1962-6. Upper: Density of undetermined, mainly young Parathemisto during a, the winter-spring months of November, January and March and b, the summer-autumn months of May, July and September. Parathemisto gaudichaudii (diamonds) or P. gracilipes (circles) was positively identified in more (large symbols) or less (small symbols) than one quarter of the months sampled. Lower: Percentage of sampling by night.

gracilipes was the only species of the genus identified (circles, Fig. 32a - upper). The main distribution at this time occurred between 55 and 57° N at a position nearer to the British than the Continental coast, with the density exceeding 0.5 specimens per sample.

Figure 32b(upper), on the other hand, shows that during the summer and autumn months in the North Sea, though most specimens determined belonged to P. gracilipes, identifications of the other species (P. gaudichaudii), though infrequent, did occur. At this time undetermined specimens were abundant from the position of the winter-spring high near the coast of Britain to a region of still greater density (more than 1.0 specimens/sample) approaching the southern tip of Norway. In addition, animals were abundant north of Ireland, where specimens nearer the coast belonged to both species, and west of France, where only P. gracilipes was recognized. Although, at this time of year, P. gracilipes was identified north of Scotland and north-west of Norway, it could not be associated here with high concentrations of undetermined specimens. Comparison with the lower charts in Fig. 32 shows that the distributions of density were unrelated to the proportion of night/day sampling.

Specimens of Parathemisto gracilipes from waters over the American shelf were identified according to the criteria set out in Table 3. They came from the Gulf of Maine-Nova Scotia-Newfoundland region on routes Eb and Nb

(see Fig. 3c); the positions and dates of sampling are as follows:

MONTH	YEAR	POSITION[1]		AREA	MEAN SPECIMENS/SAMPLE in the statistical square sampled
		$^{o}_{N}$	$^{o}_{W}$		
Jul	63	43.5	64.0	E10	0.5
Aug	63	43.5	66.0	F10	0.2
Aug	63	44.5	62.0	E10	0.3
Aug	63	42.5	68.0	F10	0.3
Mar	64	43.5	44.0	F8	0.5
Sep	64	42.5	68.0	F10	0.3
Oct	64	43.5	52.0	E9	0.3

As with examinations of material from the North Sea and vicinity, specimens sampled from this region were counted in their entirety without reference to category estimates. Consequently densities between these areas may be compared. On the American side P. gracilipes was rare at 0.03 specimens/sample in contrast to both P. gaudichaudii identified in the same samples (0.9 specimens/sample) and P. gracilipes recognized in collections from the main North Sea population (about 2.0 specimens/sample).

[1] "Position" is the approximate centre of the "statistical square" of collection.

F3.2 Distribution of Parathemisto gaudichaudii

In contrast to Parathemisto gracilipes, P. gaudichaudii is very extensively distributed and occurs primarily in oceanic waters, densities being generally high in southern subarctic waters (Fig. 30b). The extremely high value off Labrador (area D9), however, probably comes from averaging results taken predominantly during periods of abundance in summer and autumn (Fig. 21). At this time waters were free from the ice which prevented collection in winter (Fig. 3, cf. a and b).

There is the suggestion, in Fig. 30b, that concentration dropped off as the species approached 1) Arctic waters west of Greenland, 2) tropical waters in the region of the Azores and 3) neritic waters over broader regions of the American and European continental shelves. The general impression is that the main population of Parathemisto gaudichaudii lives in a broad band of subarctic water extending eastward from Labrador. Figure 1 would suggest that the Labrador Current has an especially strong influence in this region. Numbers appear to decrease in the east where the North Atlantic Drift branches north-eastwardly and in the north where subarctic water is further diluted with both polar and Drift water.

Figure 30c indicates that undetermined specimens of Parathemisto, which in subarctic water represent the young

of P. gaudichaudii (Fig. 29, Psp and Pcg), shared the same general distribution as outlined in Fig. 30b for the total specimens attributed to this species. The band of abundance, however, was more restricted both latitudinally (between 52 and 55° N) and eastwardly; in comparison, the young were noticeably fewer toward Iceland and the region linking Iceland and Spain (Fig. 30c). The shape of this distribution would lead one to suspect that breeding occurred predominantly in those waters of the subarctic gyre which originate from the Labrador Current (cf. Fig. 1). Outside of this region, particularly in the north and east, reproduction would appear to be less.

In August and September the main population of young Parathemisto in subarctic water (Fig. 31, Parathemisto undetermined) was larger and further north than on average (cf. Fig. 30c). The larger numbers are expected during this period of increased abundance (Fig. 21) and the shift in distribution is compatible with the difference in timing of seasonal maxima between hyperiids off Newfoundland and Labrador (closed circles D7, D8 and E8, Fig. 22) and those in the vicinity of Greenland and Iceland (cf. B5, B6 and B7). Also, at this time of year, fewer young than average appeared south of Newfoundland, where the southward branch of the Labrador Current extends. This suggests that there was a withdrawal of breeding in the south-west, coincident with extension of reproduction into the north. That is, the spawning areas moved northwards as the season advanced. This latitudinal progression, however, was not associated

with sea-surface temperature which was much the same in all areas and which did not increase monthly in a way correlated with the timing of propagation (cf. open circles, Fig. 22).

Parathemisto gaudichaudii rarely occurred in the North Sea (Fig. 31, diamonds) though it was found in the adjacent North Atlantic, often among concentrations of specimens unidentifiable as to species. During winter and spring, animals found with specimens recognized to be of this species were numerous off northern Norway, but not in surrounding areas. In summer and autumn, on the other hand, numbers were conspicuous north of Scotland, north of Ireland and west of France. Off the north of Scotland and the north of Ireland P. gaudichaudii was often identified among specimens further from shore while P. gracilipes was more frequently present near shore. Off France gracilipes was recognized but only nearer to shore; those numerous specimens offshore included none that could be positively identified. Most likely these and most other undetermined animals encroaching from the oceanic side were the offspring of P. gaudichaudii.

As mentioned previously regarding identification of Parathemisto, small specimens in particular tend to have the diagnostically important margins of their uropods damaged by the flattening effect of the mechanism for continuous sampling (section D2). Even though Parathemisto gaudichaudii is the larger, and therefore more readily identifiable, of the two common species, it was recognized only intermittently in samples

TABLE 16 -- Occurrences of Parathemisto gaudichaudii in surface waters of the North Sea (standard areas B1, B2, C1, C2, D1 and D2) during alternate months from January 1962 to January 1967. Position, here, is the approximate centre of the "statistical square" of collection.

MONTH	YEAR	POSITION °N	POSITION °E	AREA	MEAN SPECIMENS/SAMPLE in the statistical square sampled
Jan	62	62.5	4.0	B1	0.3
Sep	63	54.5	2.0	D2	0.5
		°N	°W		
Sep	64	59.5	2.0	B2	0.3
Nov	64	53.5	0.0	D2	0.5
		°N	°E		
Sep	65	62.5	4.0	B1	2.0
May	66	56.5	0.0	C2	0.8
		°N	°W		
May	66	56.5	2.0	C2	2.0
		°N	°E		
Jul	66	56.5	4.0	C1	0.2
Jan	67	57.5	4.0	C1	0.5

collected from the North Sea. Collections of the CPR, examined for thirty-one alternate months from January 1962 to January 1967, revealed only nine isolated cases where P. gaudichaudii occurred at the 10 m depth sampled (Table 16). A further incidence was shown in samples of the Hardy Indicator (brought to my attention by collegues Mr D. Forsyth and Mr G. Cooper and collected by the research vessel SCOTIA of the Department of Agriculture and Fisheries for Scotland in November 1966 from those statistical squares

of area B2 which are centred at 57.5°N, 0.0° and 57.5°N, 2.0°E). In these collections, however, specimens were few.

On two occasions, nevertheless, great concentrations occurred off the Yorkshire coast of England: on one, very large numbers of P. gaudichaudii were found in the stomachs of cod during June and on the beaches in July, 1966, while at another time similar amounts, containing four-fifths of this species, were present on the beaches in January 1967 (specimens courtesy of J.S. Gray). Undoubtedly these animals had been swarming and, as their composition indicated (Gray and McHardy, 1967), had been breeding. Despite the conspicuous presence of the species gaudichaudii on these occasions, the CPR collections from this and other areas of the North Sea had not revealed its increased incidence. Presumably the aggregations off Yorkshire represented localized swarmings, restricted in space and time. It is unexpected for P. gaudichaudii to have been swarming in a region where it is normally rare.

F4 Variations in Parathemisto gaudichaudii

Length frequencies were determined from samples selected to represent the varying population structure of Parathemisto gaudichaudii within two areas (details, section E3). Material from this and other sources in the CPR collections were analysed also for morphological development and sexual maturity which, as shown earlier (section E3), tend to

increase in larger animals.

Figure 33(overall) demonstrates that, for the most part, bigger specimens were fewer than smaller ones. As shown for Parathemisto gaudichaudii from New Zealand waters (Kane, 1963), those up to at least 2.2 mm are normally found in the brood pouch of the parent female. Although the category of peak frequency in Fig. 33 (2.0-2.9 mm) should therefore have included the smallest animals likely to be present in the plankton, the samples taken by the CPR contained ones which were still smaller, between 1.0 and 1.9 mm. Some or all of these very small animals probably appeared because the sampling proceduce had forced them from the brood pouches of adult females being captured. With the exception of this artifact of sampling, Fig. 33(overall) indicates that specimens became progressively less frequent with increasing length.

F4.1 Temporal variations

As shown earlier (section F1.3), fewer hyperiids were collected by day than at night. Figure 33 (night/day) demonstrates, from length measurement, that this effect was less marked among small specimens of Parathemisto. On the other hand, animals of medium to large size were strikingly less numerous by day, and can be considered to have been among those contributing most to the diurnal variation in numbers.

A similar result is found from examination of morphological development and sexual maturity. In July

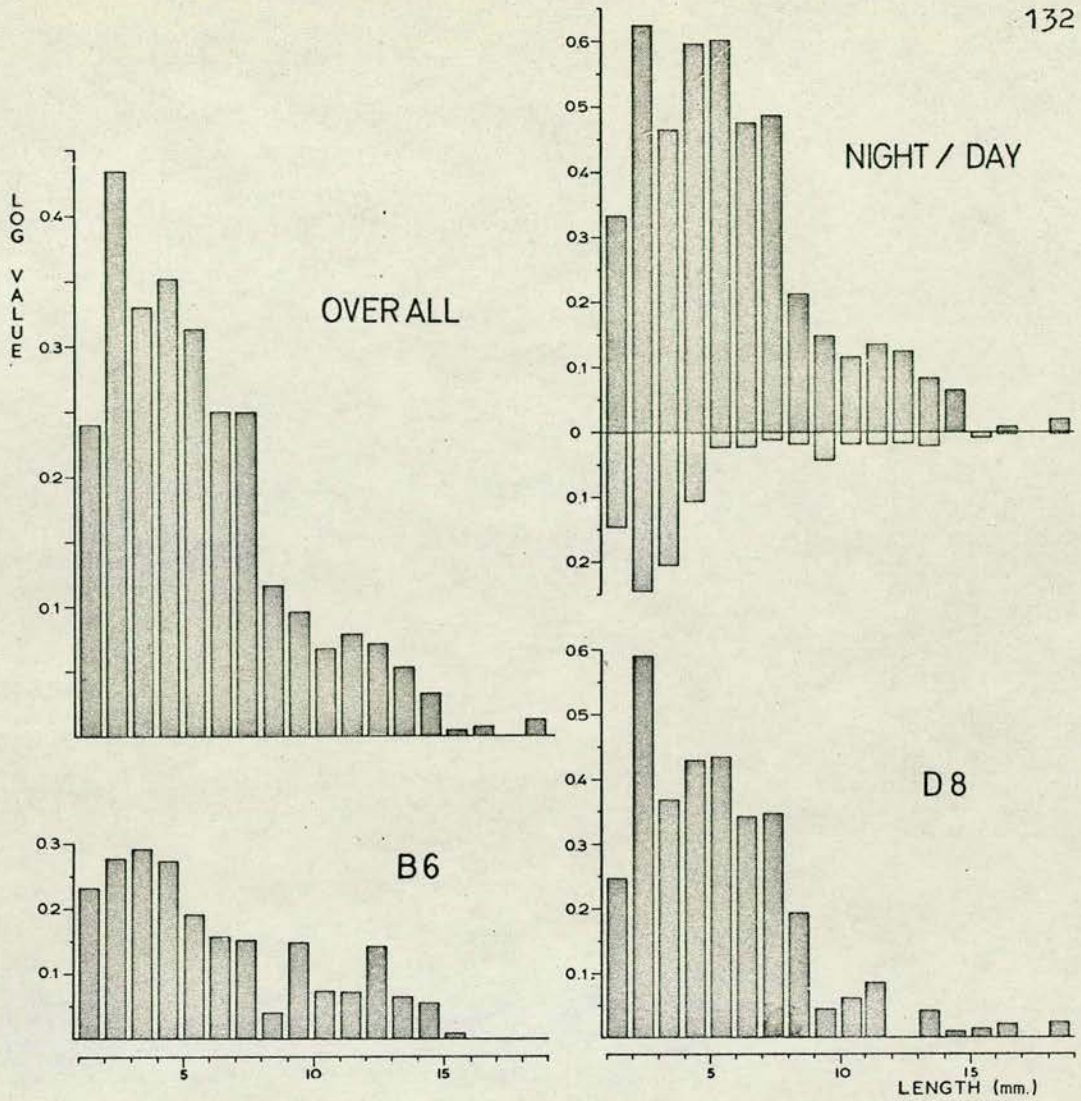

FIGURE 33 -- Length frequencies of Parathemisto: overall, night (above) and day (below), and areas B6 and D8.

From samples taken at night and by day in April, July, September and November, 1962-5, from surface waters in standard areas B6 and D8.

1963, for example, when four statistical squares east of Labrador[1] were sampled especially often, collections showed a diurnal difference in composition:

Time of day	Number of specimens examined	Percentage differentiated	
		to form	to sex
NIGHT	113	79	52
DAY	24	8	0

As for those of medium to large size (Fig. 33, night/day), specimens that could be sexually differentiated or recognized as belonging to one form or another (i.e., bispinosa or compressa) were found to be relatively less numerous by day.

The size frequency distributions in the two subarctic areas, B6 and D8, are plotted for each of the four months for which data are available (Fig. 34). In April most specimens were small, less than 5 mm long. In July the majority were over 5 mm and the larger size groups, from 10 to 19 mm, were well represented. By September, however, there was a marked change; the great majority of specimens were small (less than 5 mm) with the peak at 2-3 mm. In November most were in the middle of the size range.

The beginning of this sequence suggests growth of

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[1]These statistical squares, near the border between standard areas C8 and D8 in the western North Atlantic, are centred east of Labrador at:

55.5°N, 46.0°W; 53.5°N, 52.0°W

54.5°N, 48.0°W; 52.5°N, 52.0°W.

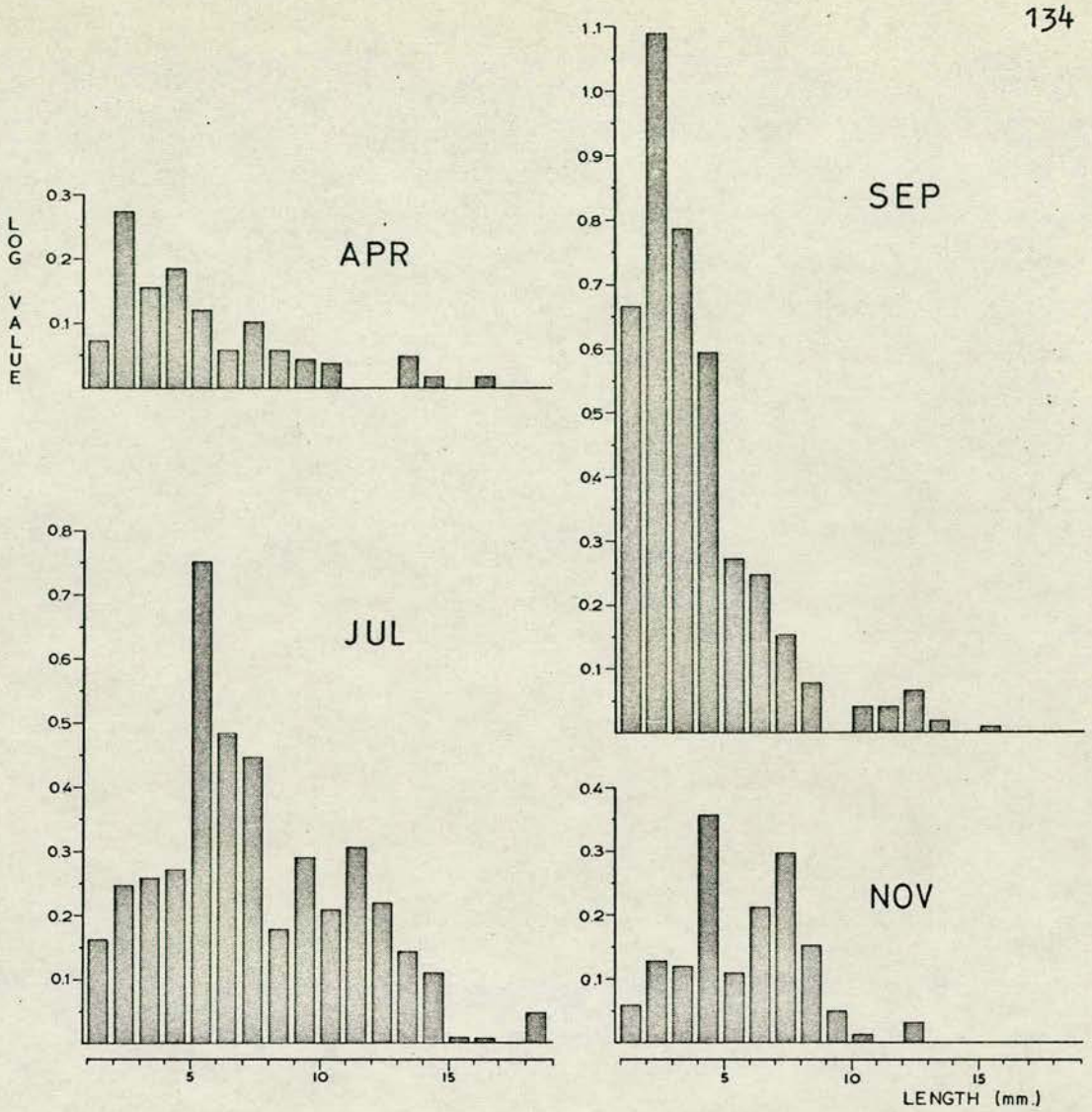

FIGURE 34 -- Length frequencies of Parathemisto, seasonal differences: April, July, September and November (for details see legend for Fig. 33).

small specimens from April to July. The greater total numbers in July, however, are not entirely accounted for through growth, even though specimens were mainly larger. Presumably the surface population was supplemented from below, perhaps by specimens that had been overwintering at a medium size such as was found in November.

Small specimens were present in all the four months but were more noticeable in April and, particularly,

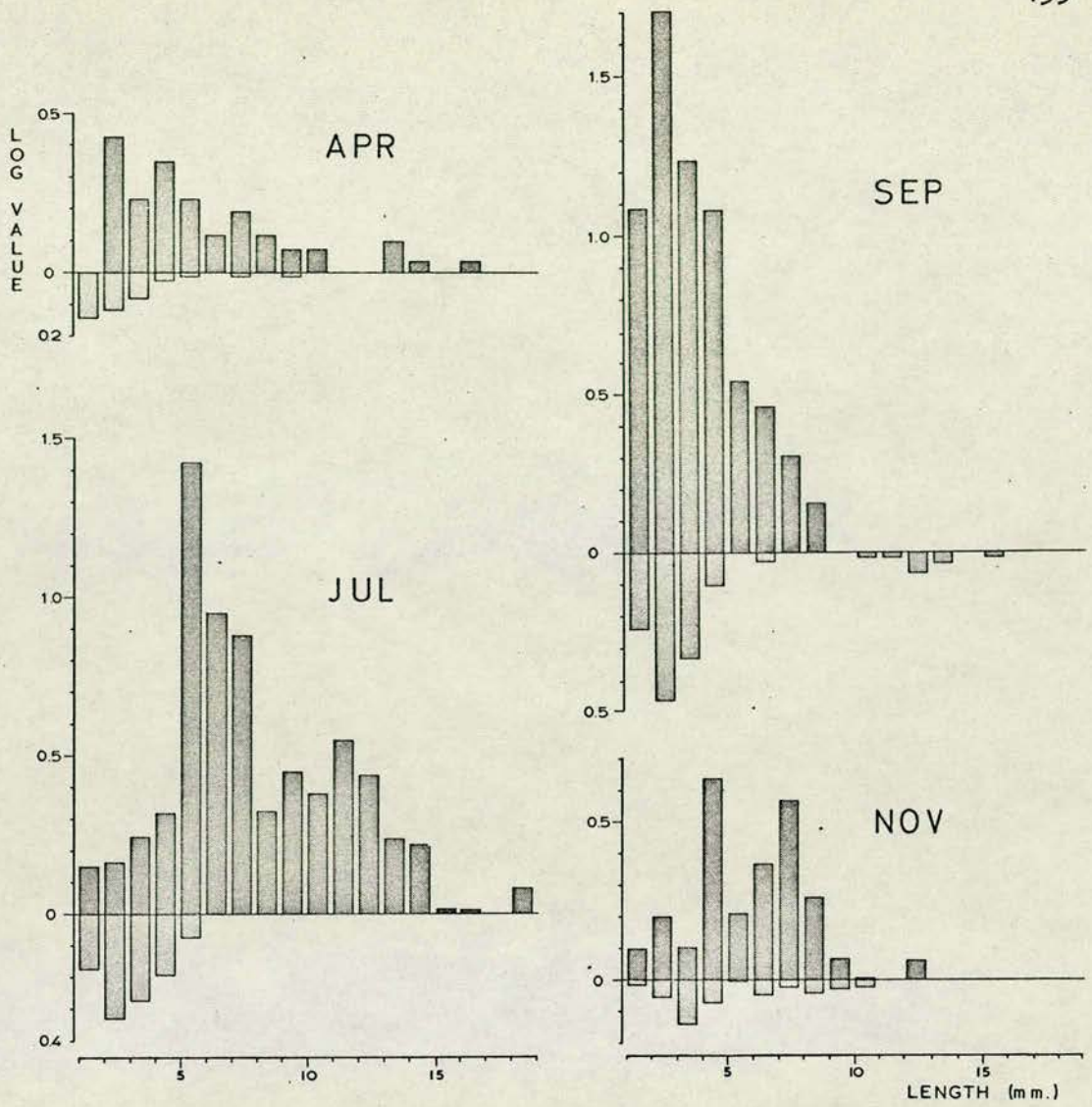

FIGURE 35 -- Length frequencies of Parathemisto, diurnal and seasonal differences: night (above), day (below) in April, July, September and November (for details see legend for Fig. 33).

in September. The great abundance of small specimens in September probably represents the offspring of the numerous large animals which appeared in July. Growth of these young may account for some of the specimens of medium size which were found in November.

According to analysis of variance (Table 17), the effect of size on the diurnal variation in numbers (S x D)

TABLE 17 -- Analysis of variance to show the relationship between specimen-size and the density of hyperiids in the surface waters of the standard areas B6 and D8 during 1962-5, particularly diurnally, monthly and by area. According to the length frequencies determined from limited samples, log values from all samples were portioned to give the data analysed (see section E3 for details). Level of significance: *=5%, **=1%.

Source	df	MSS	%MSS
Size (S)	17	50,705**	6.1
Diurnal (D)	1	462,722**	56.0
Month (M)	3	87,087**	10.5
Area (A)	1	41,137**	5.0
S x D	17	23,369**	2.8
S x M	51	18,096**	2.2
S x A	17	9,576*	1.2
D x M	3	35,786**	4.3
D x A	1	46,613**	5.6
M x A	3	15,083*	1.8
S x D x M	51	12,864**	1.6
S x D x A	17	5,669	0.7
S x M x A	51	6,421	0.8
D x M x A	3	6,725	0.8
Total	287		
Error	51	4,185	0.5

differed between months (S x D x M). As indicated previously, the animals that contributed mainly to this effect were of medium to large size. Figure 35 shows that, whereas in July specimens under 5 mm in length were similarly numerous by day and by night, in April and September they were notably fewer by day.

Thus, the diurnal behavior which caused specimens to leave the surface during the day seems, for the small ones, to have varied seasonally. This is in contrast to

that shown for large specimens. Those over 5 mm, though present at night, were nearly absent during the day, in all of the four months. Though, in April and September, a proportion of the young appear to have left the surface waters by day, they failed to do this to the extent practised by the larger animals. When, in July, the larger specimens were most plentiful, the tendency of the young to follow them in their diurnal vertical migrations was least.

Examination of morphological development suggests a seasonal cycle of vertical migration and breeding similar to that indicated by measurement of length. In the same material examined for length frequency (Fig. 36, months for two areas, 1962-5), the young specimens (in this case 3 mm or shorter) were dominant in April and, especially abundant in September but in July were exceeded by similar numbers of specimens over 3 mm in length, including both juveniles and older forms (Fig. 36, undifferentiated and differentiated).

Further information on morphological development, covering eight areas for seven months in 1965 (Fig. 36, Months for eight areas, 1965), gives a slightly altered picture of seasonal events. Whereas an increase in total numbers from March to May could be attributed to both large and small animals, the major population growth, which occurred from May to July, was largely due to the appearance of young (3mm or shorter). Thus while in the

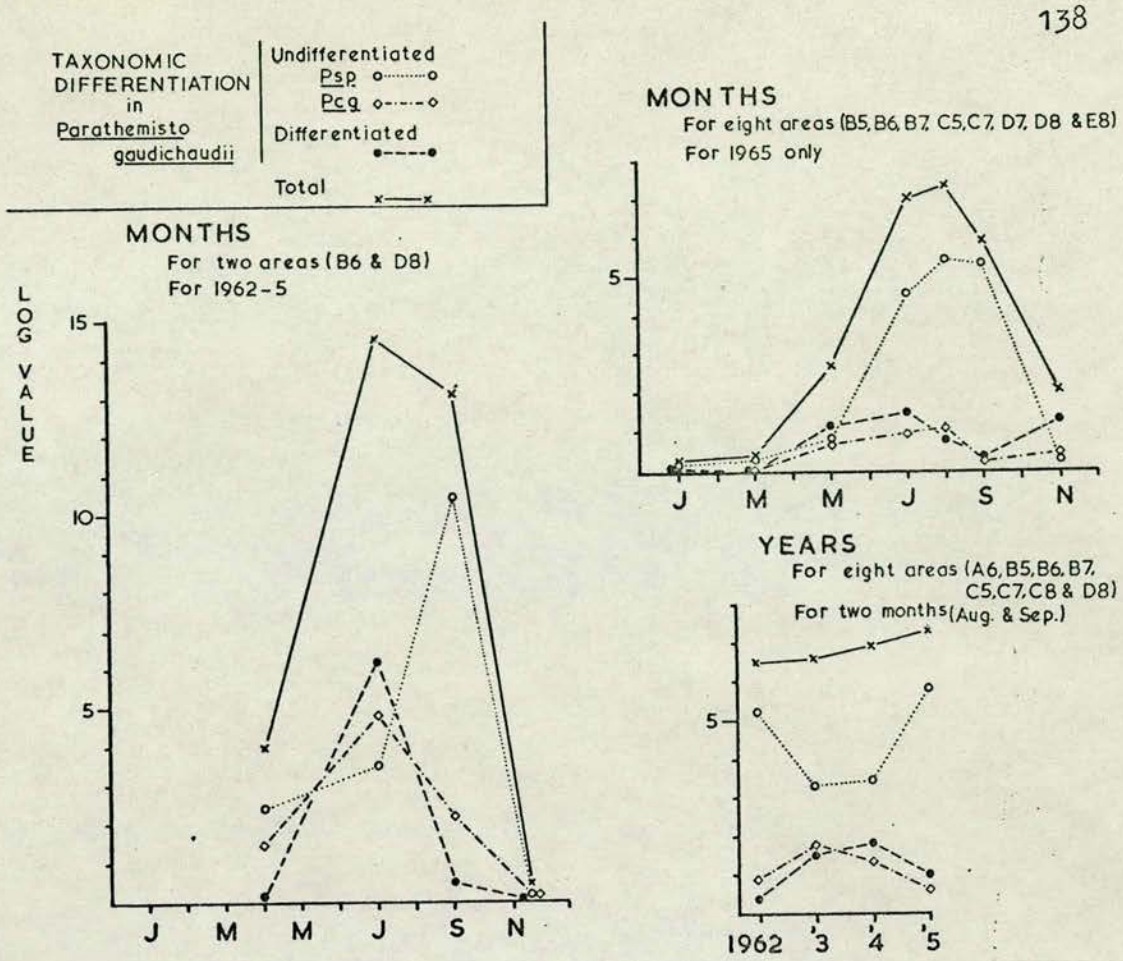

FIGURE 36 -- Relative densities of the three categories of morphological differentiation of Parathemisto for 1) MONTHS for two areas and four years, 2) MONTHS for eight areas and one year and 3) YEARS for two months and eight areas. Densities have been adjusted to account for the differing length-frequency distributions represented by the various categories. (Figure 29 demonstrates the unequal ranges of length among categories and section E3 gives the method by which densities are adjusted.)

four years 1962-5 hyperiids living in the two subarctic areas may have bred mainly between July and September (Fig. 36, Months for two areas, 1962-5), those occupying other areas, in both subarctic and Drift regions during 1965, seem to have bred most intensively between May and July.

TABLE 18 -- Relative densities of Parathemisto in the three categories of morphological differentiation for the months of August and September, 1962-5. Mean log values for standard areas A6, B5, B6, B7, C5, C7, C8 and D8. Densities have been adjusted to account for the differing length-frequency distributions represented by the various categories. (Figure 29 demonstrates the unequal ranges of length among categories and section E3 gives the method by which densities are adjusted.)

	Psp		Pcg		Pc+Pbc+Pb		Total	
	AUG	SEP	AUG	SEP	AUG	SEP	AUG	SEP
1962	5.1	3.3	1.1	0.5	0.8	2.1	7.1	6.0
1963	3.9	2.0	0.8	2.7	2.7	1.0	7.4	5.7
1964	3.3	3.7	1.9	0.7	2.5	1.6	7.8	6.0
1965	5.9	5.3	1.1	0.2	1.6	0.4	8.6	5.9

In these additional areas, larger specimens were numerous from May to August in 1965 but decreased markedly in September, as did those in the two subarctic areas during 1962-5. Here, however, the relative numbers of young in July had far exceeded those of the older animals whereas in the two areas, the young of this month were comparatively fewer.

As shown in Fig. 36(Years), though total numbers changed little between the four years 1962-5, the relative proportions of young and older Parathemisto seem to have varied notably, at least when the months of August and September are compared. Although general variations in population structure may have occurred between years, it seems more likely that these proportional differences

merely reflect annual shifts in the timing of seasonal events. Table 18 shows that between August and September the age composition did, in fact, vary annually. Within the limits of the data, however, it is not possible to suggest the significance of these changes.

F4.2 Geographical variations

In Table 17, size composition is shown to have varied between the subarctic areas B6 and D8 (S x A). Comparison of length frequency distributions for these areas (Fig. 33), suggests that specimens less than 10 mm long were proportionately more numerous off Newfoundland (area D8) than off Iceland (B6). A similar picture is indicated by comparison of horizontal distributions for specimens in different stages of morphological development (Figs. 37-46).

Figures 37 to 41 illustrate, for 1965, the seasonal changes in horizontal distribution of specimens belonging to each of the five categories of morphological differentiation. Whereas in winter and spring most animals were confined to surface water over and nearby the Grand Newfoundland Banks, by summer their distributions had extended well into the remaining subarctic waters and into the colder regions of the North Atlantic Drift. In autumn, when they had become much fewer generally, occurrences were scattered. Figures 42 to 46 indicate distributions during August and September of 1962, 1963 and 1964. These geogra-

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FIGURES 37-41 -- Geographical distribution and centres of distribution for the density of Parathemisto in surface waters of the North Atlantic (North Sea and vicinity excluded) during seven months of 1965, separating the five categories of morphological differentiation in taxonomic character (but not correcting densities for size range -- explanation in section E3):

Psp -- FIGURE 37
Pcg -- FIGURE 38
Pbc -- FIGURE 39
Pc -- FIGURE 40
Pb -- FIGURE 41

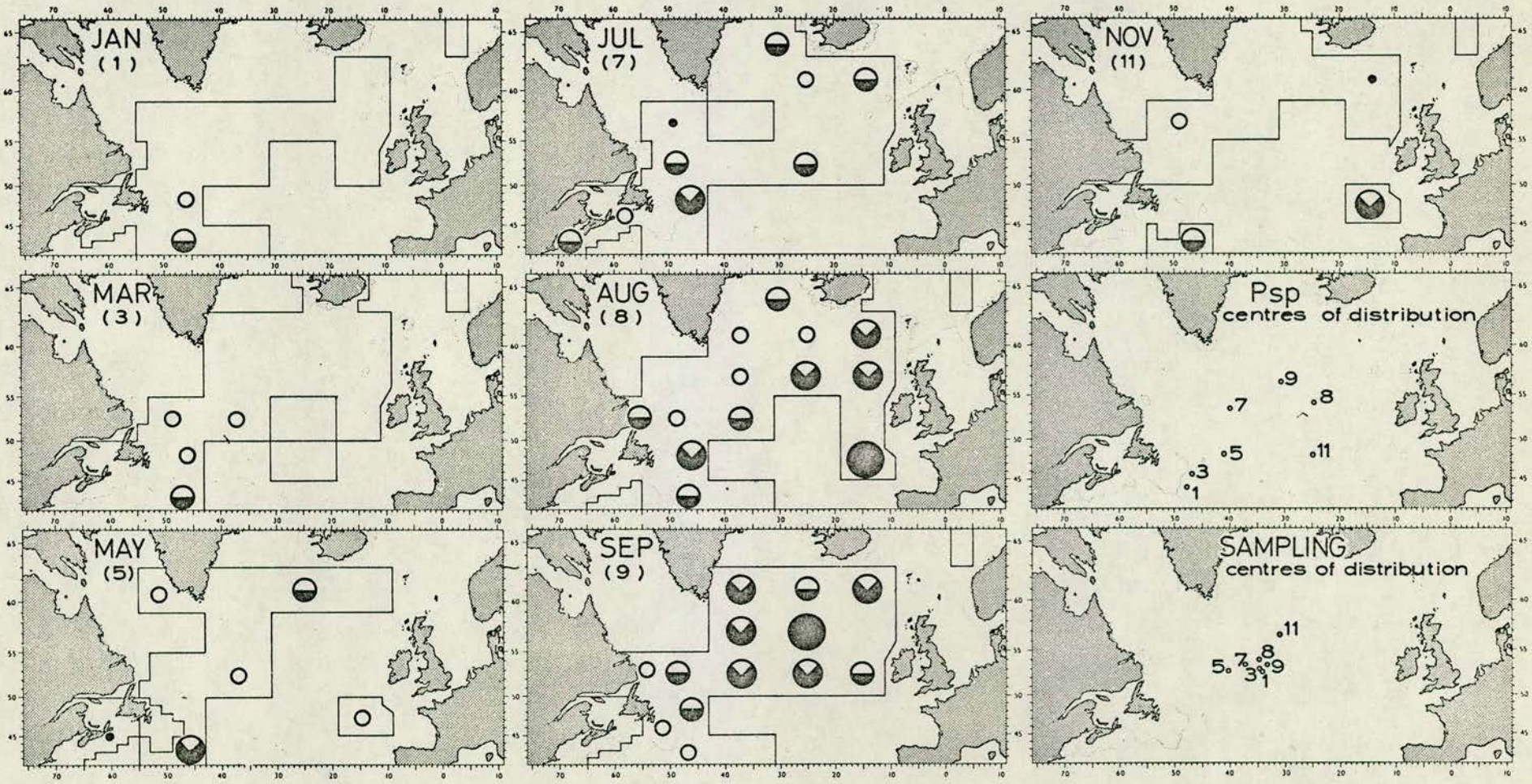

FIGURE 37 -- (Psp): Legend on preceding page.

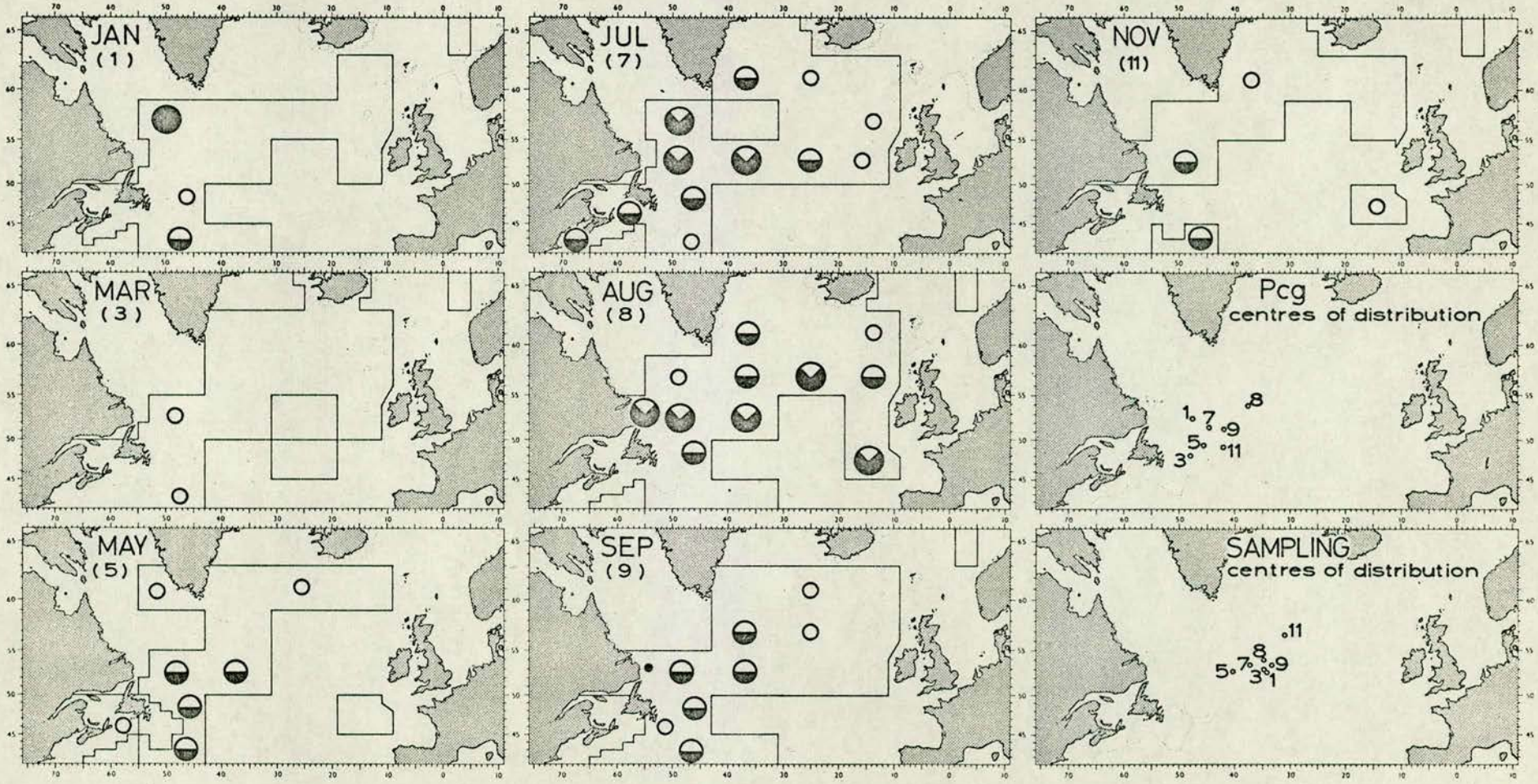

FIGURE 38 -- (Pcg): Legend on page preceding Fig. 37.

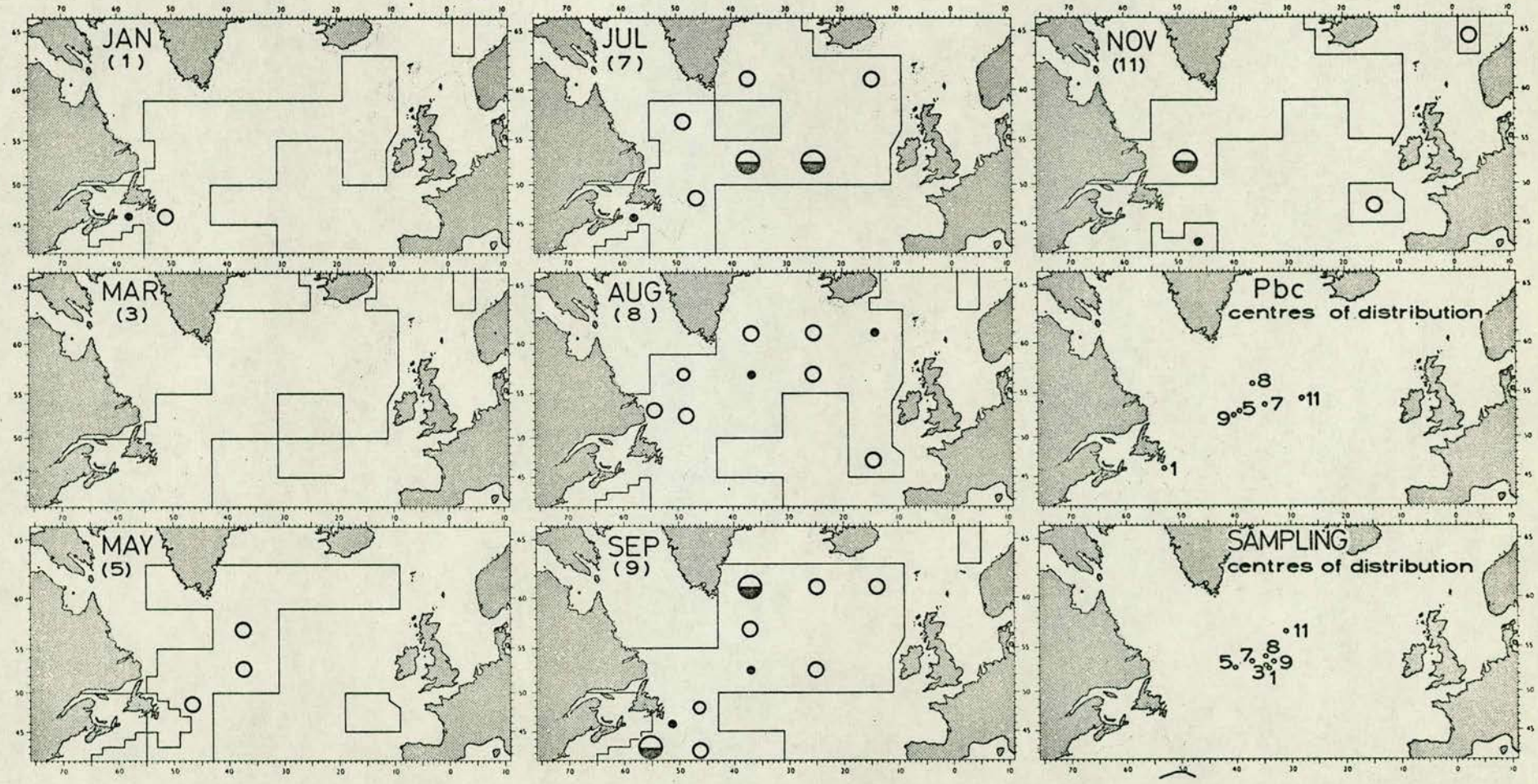

FIGURE 39 -- (Pbc): Legend on page preceding Fig. 37.

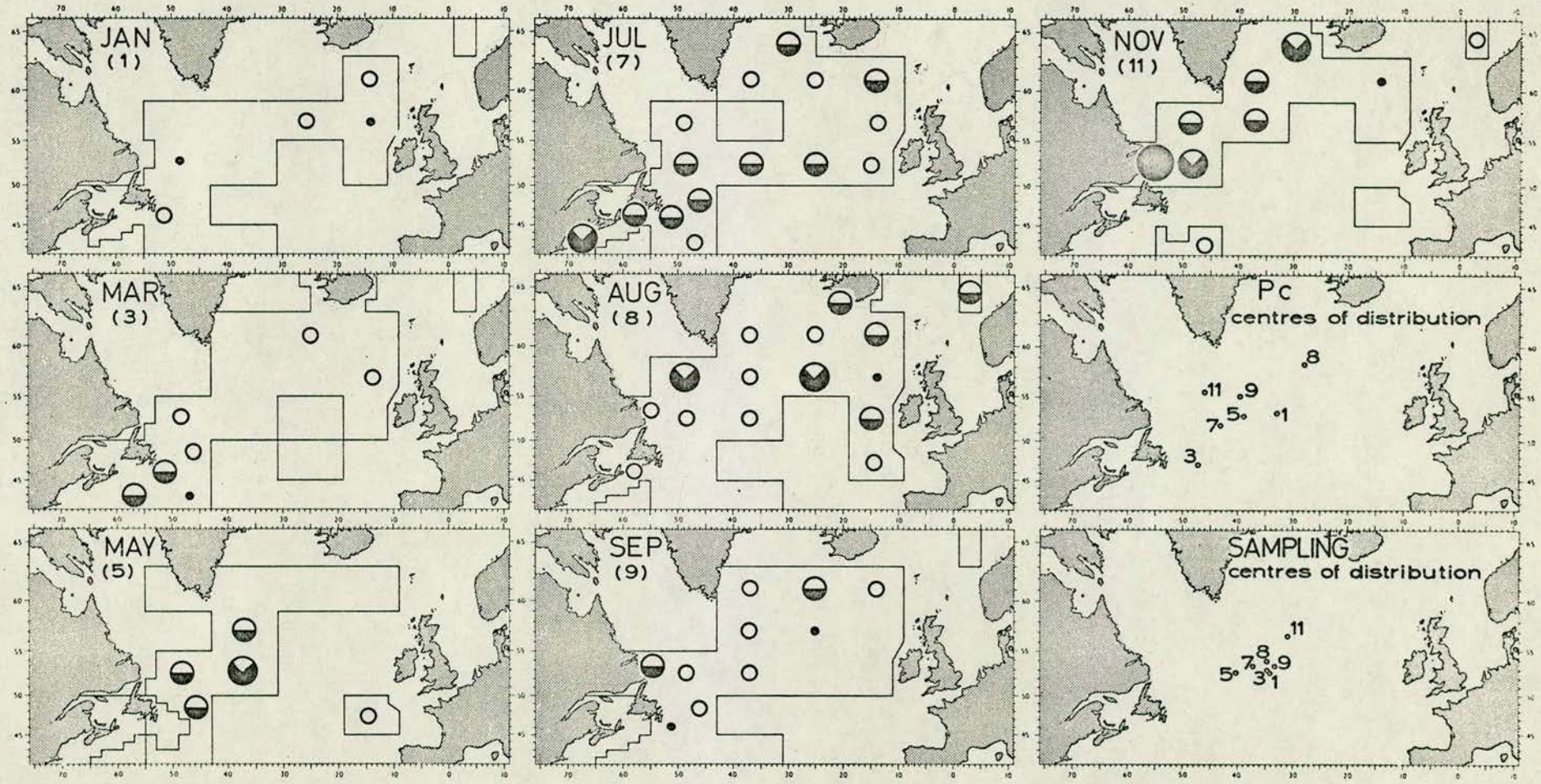

FIGURE 40 -- (Pc): Legend on page preceding Fig. 37.

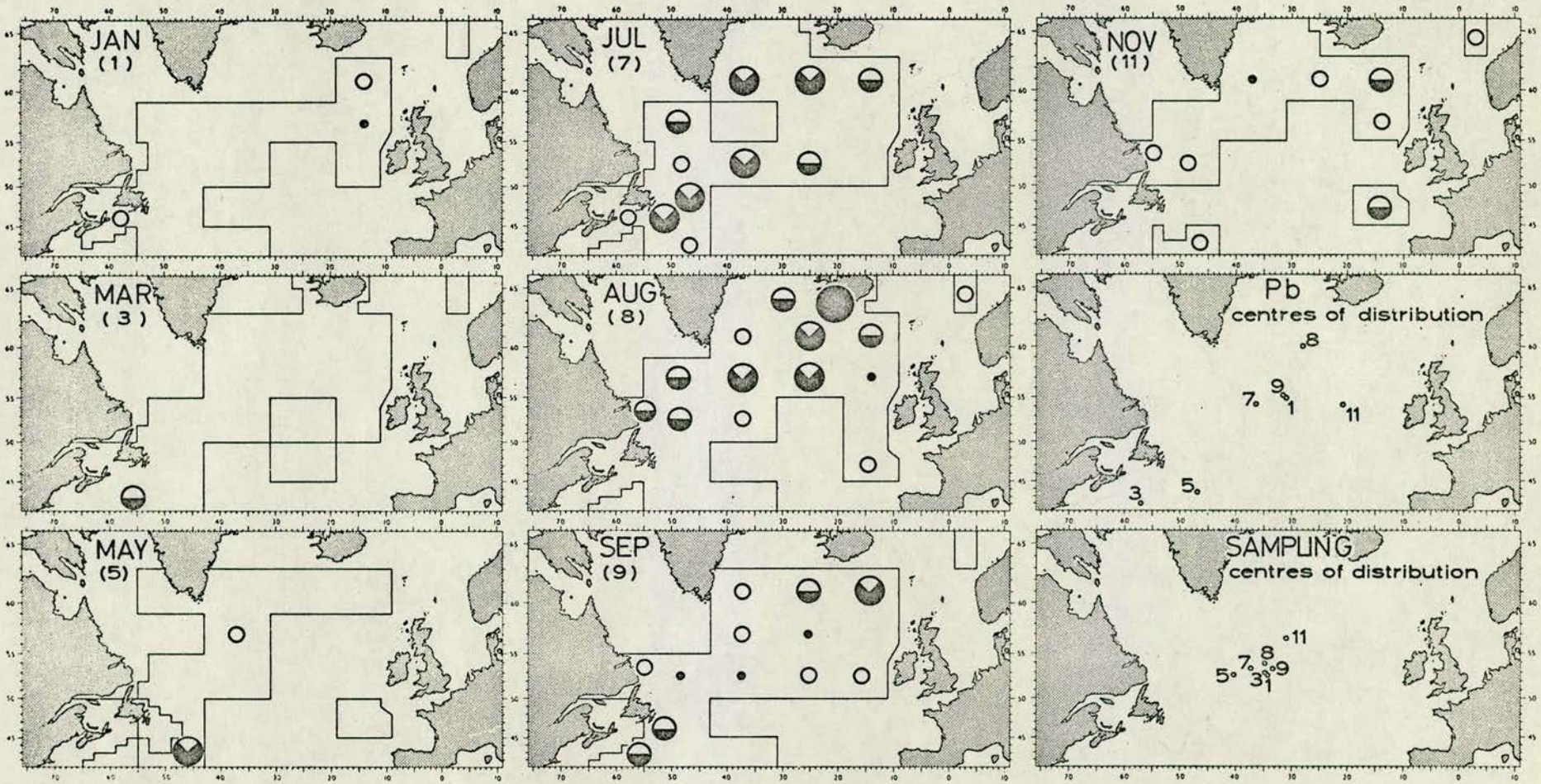

FIGURE 41 -- (Pb): Legend on page preceding Fig. 37.

FIGURES 42-46 -- Geographical distributions and centres of distribution for the density of Parathemisto in surface waters of the North Atlantic (North Sea and vicinity excluded) during August and September of 1962-4 (distribution during August and September of 1965 in Figs. 37-41), separating the five categories of morphological differentiation in taxonomic character (but not correcting densities for size range -- explanation in section E3):

Psp -- FIGURE 42
Pcg -- FIGURE 43
Pbc -- FIGURE 44
Pc -- FIGURE 45
Pb -- FIGURE 46

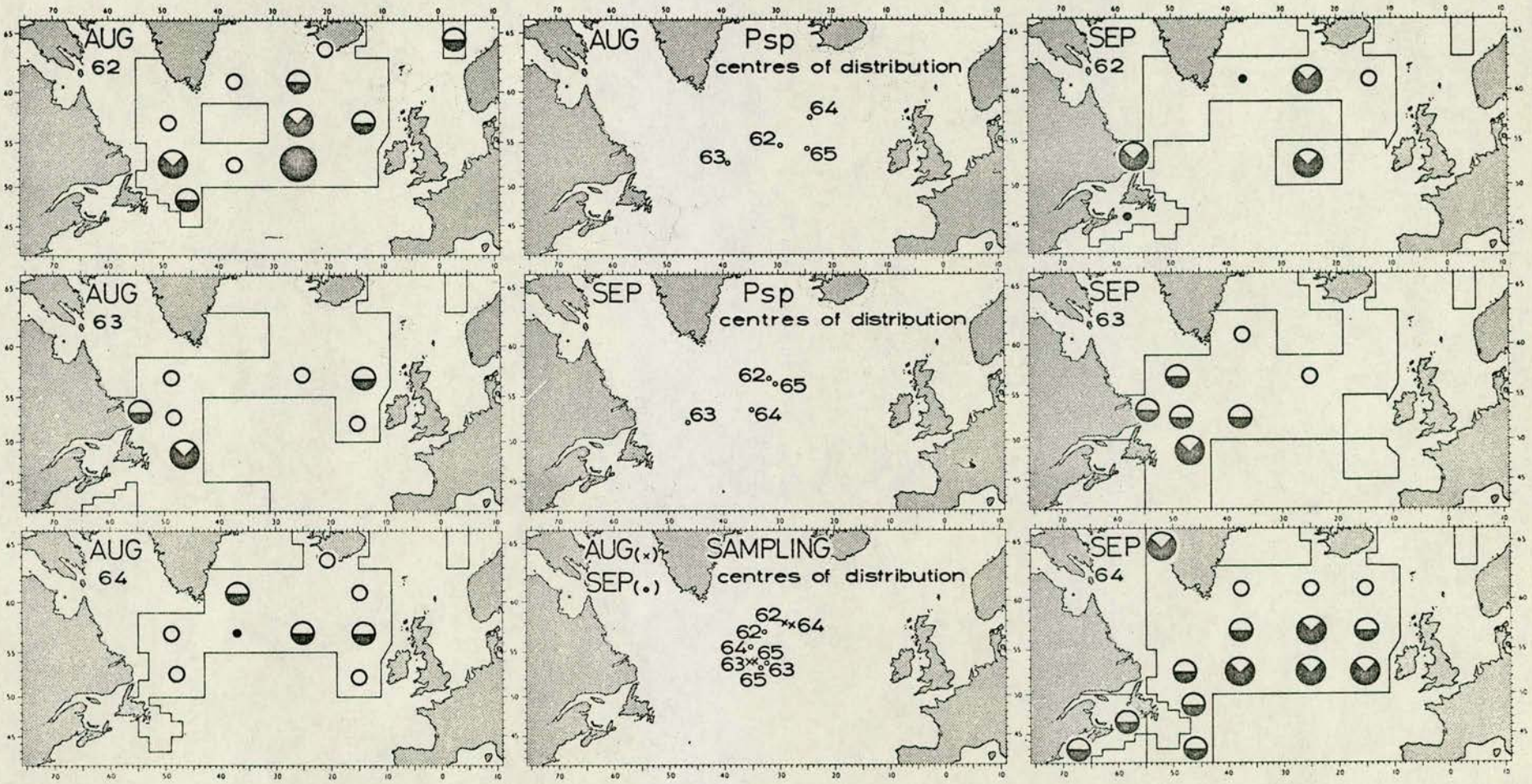

FIGURE 42 -- (Psp): Legend on preceding page.

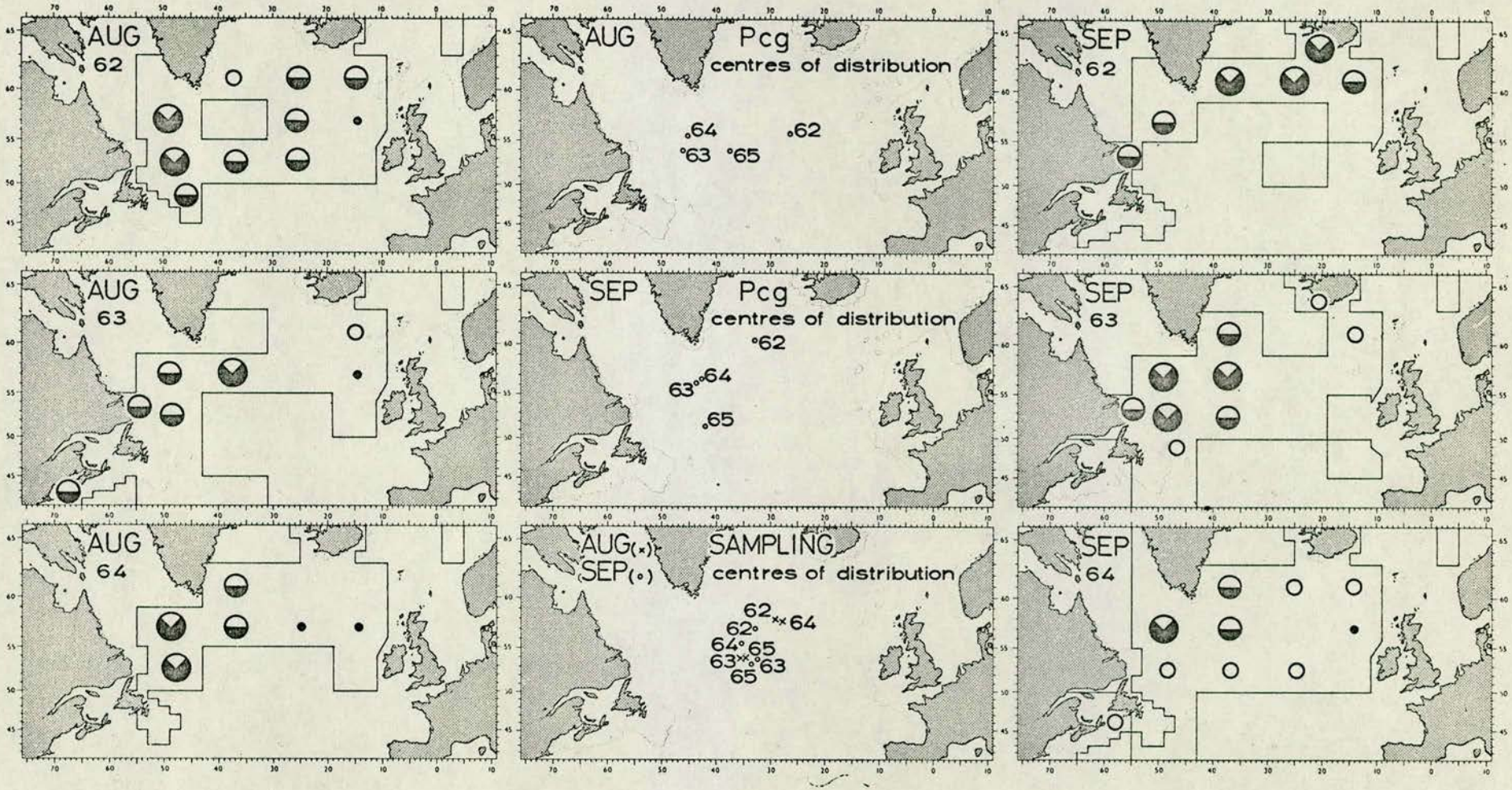

FIGURE 43 -- (Pcg): Legend on page preceding Fig. 42.

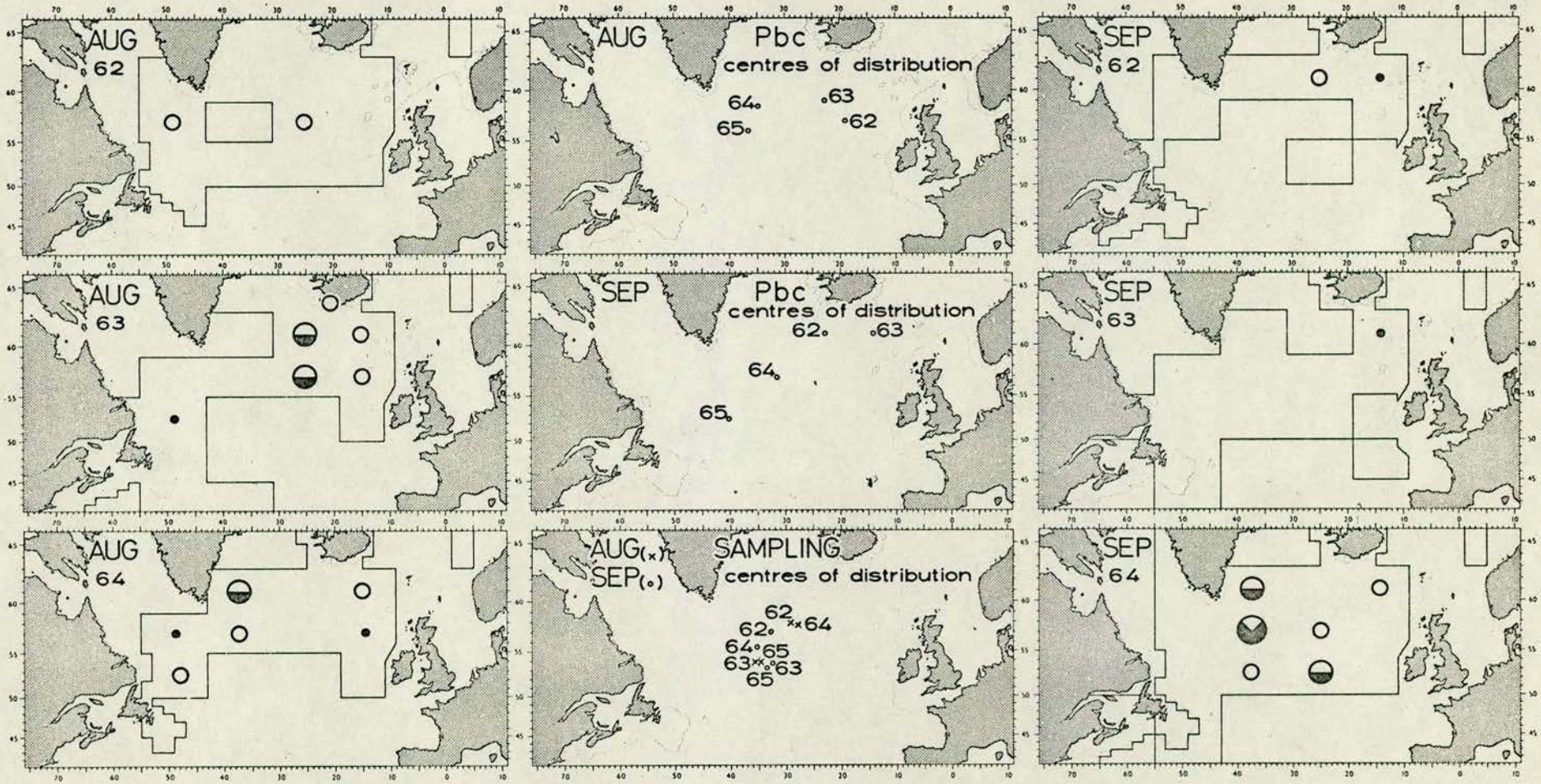

FIGURE 44 -- (Pbc): Legend on page preceding Fig. 42.

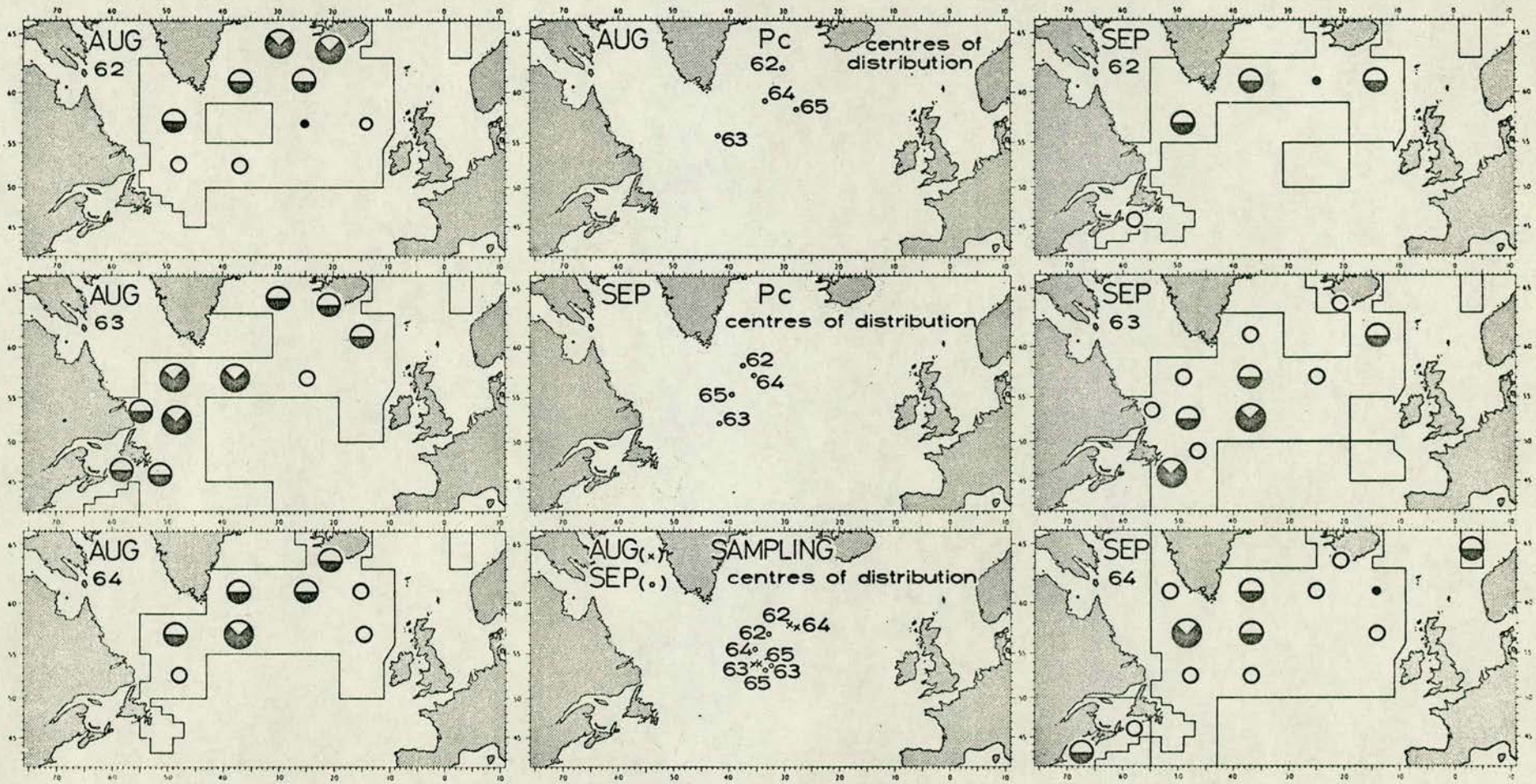

FIGURE 45 -- (Pc): Legend on page preceding Fig. 42.

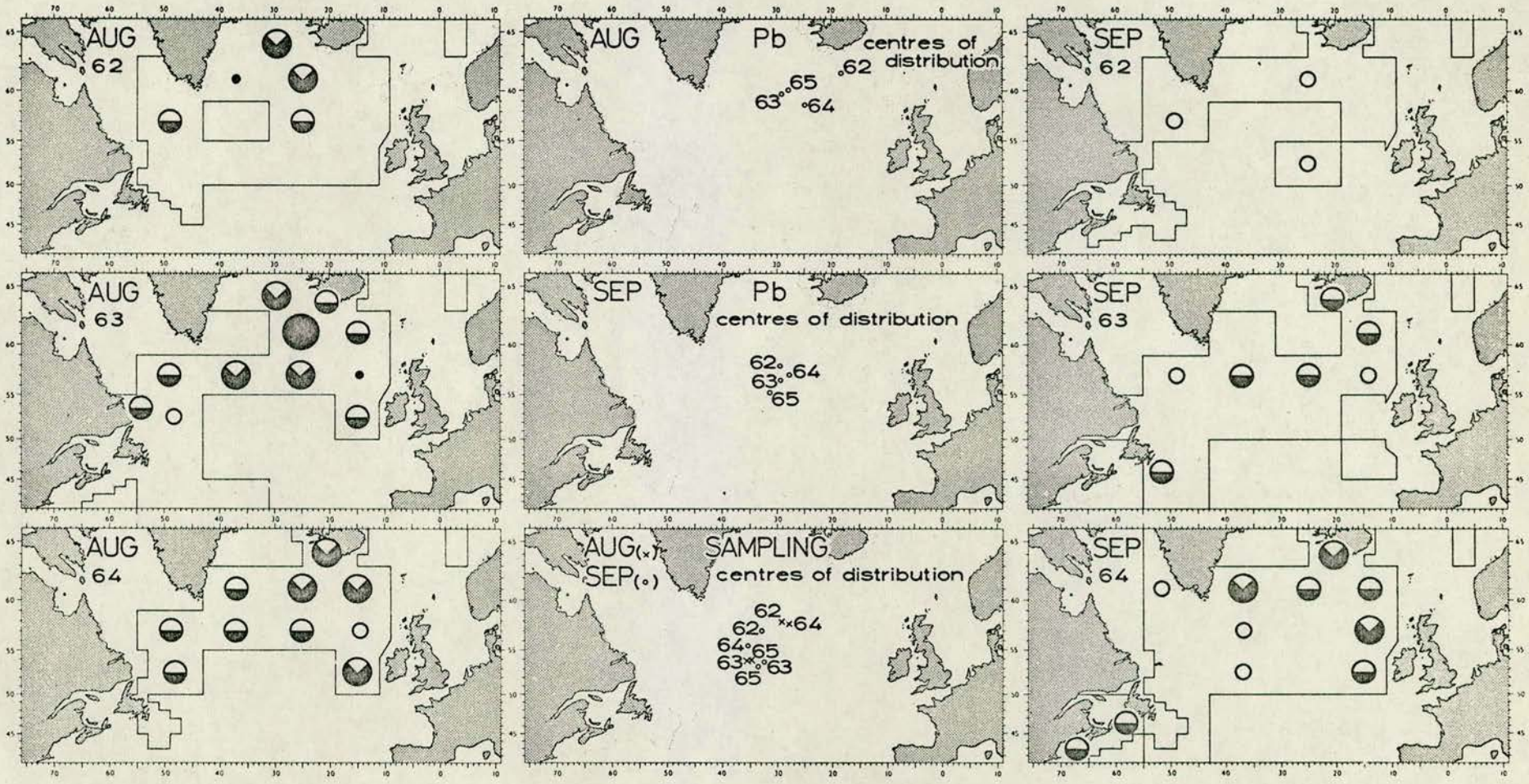

FIGURE 46 -- (Pb): Legend on page preceding Fig. 42.

phical patterns and those for the same months in 1965 (Figs. 37-41) may be compared and possible variations between years suggested. Centres of distribution are shown for all four years, including 1965.

For each category of development, the seasonal change in distribution during 1965 took slightly different geographical patterns. When, in January, the young (Psp, Fig. 37) were least numerous, they were confined to waters of the Labrador Current (cf. Fig. 1) east of the Grand Newfoundland Banks. As these became more abundant, however, their distribution spread. By May and July young appeared in shelf waters south of Newfoundland and in most oceanic waters across to the eastern North Atlantic. When, in August and September, numbers were greatest, most of the subarctic and Drift regions were populated, although shelf regions south of Newfoundland seem to have been abandoned. In November, however, specimens had become fewer and the distribution of many of the young was again restricted to lower latitudes.

The monthly centres of distribution shown for Psp in Fig. 37 (numbers refer to months, eg. January (1), February (2)) give a simplified indication of the seasonal shifts in distribution. To check that changes of distribution of Parathemisto were not due to gross alterations in sampling distribution, centres for each are compared (cf. centres of distribution for Parathemisto and for sampling, eg. Fig. 37).

The distribution of young during years other than 1965 suggests some differences between years. Though generally the regions of occurrence were similar, in 1963 animals in the west appeared in relatively greater abundance, particularly off Labrador and Newfoundland, for both August and September (Fig. 42).

Specimens slightly further developed (Pcg, Fig. 38) were least numerous in March of 1965 and, at this time, as with the young, occurred mainly west of the Newfoundland Grand Banks. Though in May they were spread northwards and eastwards, relatively few appeared in the eastern Atlantic. Only in August were these growing specimens dispersed very far. Again in September and November the majority occurred in the western North Atlantic. Centres of distribution (Fig. 38) when compared with those of the young (cf. Fig. 37) emphasize the concentration of developing specimens in the west. This observation is similar to that shown by length measurements, where relatively more small and medium size specimens occurred north-east of Newfoundland (area D8, Fig. 33) than south-west of Iceland (B6).

As in the year 1965 developing specimens (Pcg) appear in the other years to have been most numerous in western regions of the North Atlantic (Fig. 43). In August and September of 1962, however, animals were also abundant south-west of Iceland. Only in August of 1965, nevertheless, were they notably apparent in the warmer waters west of France (cf. Fig. 38).

In 1965, animals of intermediate form (Pbc) appeared in small numbers over the Newfoundland Banks and the St. Lawrence estuary in January; they were not found in March but in May occurred in limited amounts in the western Atlantic. From July to September they appeared at scattered locations over the survey area. In November, however, occurrences again became restricted to more southern latitudes, both around the Newfoundland Banks and west of France (Fig. 39).

In August and September of 1962-4, occurrences of the intermediate form (Pbc) were scattered, as in 1965, over the North Atlantic (Fig. 44). Though in September, 1965, they were noticeable south of Newfoundland (Fig. 39), numbers were generally fewer off both western and eastern seaboards than in the region intervening.

Unlike the less well developed forms, those of Parathemisto gaudichaudii recognizable as to bispinosa or compressa forms were found to be present in the north-eastern North Atlantic during their period of scarcity (January)(Figs. 40 and 41). In March, however, concentrations appeared mainly in the region of the Grand Banks. In May numbers occurred further to the north and east and by July both forms had populated the greater part of subarctic water. In the months following, however, distributions of the two forms seem to have diverged.

During August, as in July, both distinct forms (Pc and Pb) were plentiful in subarctic and Drift regions of the North Atlantic and their distributions were similarly

centred (cf. Figs. 40 and 41, with reference to centre of distribution No. 8). In September, however, whereas form compressa appeared abundantly between Newfoundland and Iceland, bispinosa was most numerous both south of Newfoundland and south-east of Iceland. This suggestion of dissimilar distributions became more noticeable in November. During this month, centres were more towards the west for compressa and further south and east for bispinosa (Centre No. 11). While the distribution of compressa remained similarly between Newfoundland and Iceland, that of bispinosa extended to include, not only the area south-east of Iceland but also a region west of France. South-east of Newfoundland, however, the numbers on this occasion were similar for both forms.

As in 1965, the August distributions of the extreme forms bispinosa and compressa were in the other years, 1962-4, rather similar. Animals were abundant principally in the subarctic region between Newfoundland and Iceland, but occasionally they were numerous in Drift regions off the British Isles, the bispinosa form most often being noticeable there; whereas the compressa form was predominant in August 1965, bispinosa was especially evident during August 1963, August and September of 1964, and August, September and November of 1965 (cf. Figs. 40, 41, 45 and 46). From the centres of distribution (cf. Figs. 45 and 46), dispersal of the two forms in August would appear to be reasonably similar during the four years.

In September, however, as was indicated in 1965, the distributions of bispinosa and compressa forms seem to have diverged. Although in 1962 numbers of bispinosa were low and the distribution not well demonstrated; in 1963, 1964 and 1965, the separation was clearly evident (Figs. 45 and 46). While compressa was most often abundant in subarctic regions between Newfoundland and Iceland, bispinosa occurred here to a more limited extent but predominantly in regions between the west of the British Isles and the south of Iceland, where mixing with Drift waters is likely to have occurred (cf. Fig. 1). In areas south of Newfoundland, both forms occurred in September 1964 though only bispinosa was apparent in September 1965.

G DISCUSSION

G1 Hyperiid genera of the North Atlantic and North Sea

As is commonly found among other taxonomic groups, species-diversity in hyperiid amphipods is less in cooler than in warmer waters of the ocean (Sverdrup et al., 1942 - p867). On both sides of the North Atlantic this phenomenon is apparent; whether north of 50°N along the European coasts (Stephensen, 1925; Vane, MS1951) or north-west of the Gulf Stream off the American coast (Grice and Hart, 1962), the species in cold waters are considerably fewer. Stephensen (1925) and Vane (MS1951) found altogether only six genera which had species apparently characteristic of colder water of the north while Grice and Hart (1962) recognized a mere three. These in total were: Typhana, Scina, Vibilia, Hyperoche, Hyperia and Parathemisto.

Typhana appears to be generally scarce so that evidence concerning its affinities is poorly understood (Stephensen, 1925). Whereas Tesch (1911) regards it as preferring surface waters in subtropical and tropical regions, Stephensen (1925) points out that specimens have been found at all levels, and mainly in cooler (and perhaps better sampled) waters off the British Isles. Scina and

Vibilia include species from both deep-sea and surface waters (Stephensen, 1925; Grice and Hart, 1962). Hyperia consists of two cold-water species belonging to the subgenus Hyperia (Dunbar, 1963) and several warm-water ones, members of the subgenus Parahyperia (Yang, 1961). Similarly within Hyperoche, species may be northern (one) or southern (two) (Stephensen, 1925). Though one species of Parathemisto does tend to occur further south than the others, all four in the North Atlantic reside mainly in cooler northern waters (Stephensen, 1925; Vane , MS1951; Bowman, 1960).

In the present survey only Parathemisto, Hyperoche and subgenus Hyperia occurred commonly in waters north of the warm-water system. For convenience therefore these, referred to as "cold-water genera", were treated separately from the others which, including subgenus Parahyperia, were termed "warm-water genera". Typhana was not collected at all and Scina and Vibilia, though represented, were not apparent in cold-water regions.

As expected, the warm-water group was distributed mainly along the Gulf Stream current and in southerly parts of the North Atlantic Drift. Nevertheless, one specimen each of two genera from this group (Lycaea and Phronima), were found in areas north of the warm system. As anticipated, most appearances of the cold-water group were scattered across the northern North Atlantic, from southern parts of the Labrador Current to the Irminger Sea. In this regard, however, those occurrences of Hyperoche south-east

of the Grand Newfoundland Banks and in the southern North Sea look suspiciously out of place, perhaps even "warm-water" in geographical position. This implies that specimens occurring in these regions might belong to warm-water species of the genus.

It would seem that little quantitative information has been lost through ignoring the specific identity of genera other than Parathemisto. Where in Gulf Stream water the "warm-water genera" were proportionally important, the number of specimens of each genus per area was very low. Further more, in subarctic waters, where numbers were great, the warm-water representatives amounted to a negligible fraction of the specimens examined. Quite possibly the contribution of the various genera to the abundance and distribution of hyperiids might have been sufficiently well understood, for the purposes of this study, by treating all those other than Parathemisto as a single group.

G2 Taxonomy of Parathemisto

Although the generic name Themisto Guérin 1825 is still used by some authors, it has been shown (Barnard, 1930) to have been twice preoccupied. Instead Parathemisto Boeck 1870 is correct. Once it was thought that there were two genera, Parathemisto and Euthemisto Bovallius 1887. This separation has since either been dropped completely (Stephensen, 1923 and 1924) or relegated to subgeneric level, subject to modified criteria (Barnard, 1930). Evans (1968a)

gives reason why even subgeneric distinction should be abandoned.

Bowman (1960) lists seven species of Parathemisto. Four of these were found in the present collection:

1) Parathemisto gaudichaudii (Guérin) in its various forms has been called Euthemisto (or Themisto) compressa (Goës), E. antarctica (Dana), E. bispinosa Boeck, E. thomsoni Stebbing and P.(E.) gaudichaudii (Guérin). Mackintosh (1934, 1937), Pirlot (1939), Dunbar (1963, 1964) and Siegfried (1965) chose to spell the specific name with a single terminal 'i'. Some of the synonyms stem from this species' having two extreme forms (a long-legged 'bispinosa' form and a short-legged 'compressa' one), plus intermediates (Stephensen, 1923; Mogk, 1927).

2) Parathemisto gracilipes (Norman), as pointed out by Stephensen (1924), has been termed also E. compressa var. gracilipes by Norman and described as a "depauperized form of E. compressa" by Brady and Norman. Until Barnard (1930) suggested that pectination of the inner margin of the endopodite of uropod three, was a definitive character, the main difference noted between this species and P. gaudichaudii was the size at maturity, P. gracilipes being smaller. Stephensen (1924), erroneously using Themisto as the generic name, showed that a species inadequately described by Kröyer as Hyperia oblivia was probably P. gracilipes. Many authors have mistakenly identified Kröyer's species with the name of another, P. abyssorum

(Stephensen, 1924). As a result, the species P. gracilipes has been called not only E. compressa but also P. oblivia and P. abyssorum.

Tesch (1911) reported Parathemisto oblivia, Euthemisto compressa, E. gracilipes and E. bispinosa from the North Sea. Stephensen (1924) suggested that P. oblivia and E. compressa of Tesch might actually be in part T. gracilipes. Vader (1967, personal communication) was able to find in the Leiden Museum, a few samples of specimens which had been identified by Tesch (1911, 1915) as E. compressa, P. oblivia and P. gracilipes. On reexamination Vader found all samples to contain only P. gracilipes.

3) Parathemisto abyssorum Boeck, as mentioned above, has been confused with P. gracilipes. Sars (1895) produced an excellent description and figure of the species, but called it P. oblivia. His observation that the basal part of the maxilliped is without distal setae does not appear to have been mentioned since as a diagnostic character. Nevertheless, it was found, in the present study, to be a useful feature if identification of a specimen was in doubt due to damage of other parts. Normally shapes of the carpus of pereopods three and four serve adequately to distinguish the species from either P. gracilipes or P. gaudichaudii.

4) Parathemisto libellula (Lichtenstein). Some authors have mistakenly attributed this species to Mandt in whose publication Lichtenstein is named as author of the

description (Bowman, 1960). Fortunately no other species or name has been confused with this animal. Basal tufts of setae on the dactyls of pereopods five to seven, which are seen readily even in small specimens, serve to distinguish it from other Atlantic species of Parathemisto.

The compressa and bispinosa forms of Parathemisto gaudichaudii were once regarded as separate species. After comparing their distributions and morphology, and considering the value of the distinguishing features listed by Vosseler, Stephensen (1924) decided to unite them as forms of a single species. Most workers since have adopted his proposal.

Mogk (1927) studied morphological variability within this species. In a sample of 100 individuals he found a number with characteristics between the two forms. Moreover he observed, as have others since (Huntsman - cited by Bousfield, 1951; Kane, 1966) that occasionally one or two strong features of each extreme form may be seen on the same specimen. In the present study, specimens displaying transitional and mixed characteristics were given a classification of their own, mainly to facilitate quick tabulation of the compressa and bispinosa forms.

Kane (1966) refers to unpublished evidence, gathered by J.A. Nicholson, that the two forms of Parathemisto gaudichaudii from the Southern Ocean may be genetically determined by a sex-linked factor in which bispinosa is dominant. Other data indicate that the ratio between

specimens of bispinosa and compressa may vary according to depth (Bigelow, 1917), distance from shore (Bigelow, 1917 and 1926; Bousfield, 1951), latitude (Barnard, 1932; Kane, 1966; Shen, MS1966) and season (Bigelow, 1926; Vane, MS 1951; Kielhorn, 1952). These variations suggest that interrelationships between the environment and the animals affect the relative abundance of these forms (for further discussion see section G4).

G3 Biology of Parathemisto

For any one species of Parathemisto, the ecological information is far from complete. However, by bringing together all findings available including some pertaining to a species (P. pacifica) not encountered in the present material, a general understanding can be achieved and relationships within the genus may be better recognized. Consequently for each topic discussed, some pertinent facts from the literature precede consideration of the results.

G3.1 Swarming

Parathemisto is well known for its swarming activity. Though in many situations, P. gaudichaudii may be collected in small numbers (Stephensen, 1924), it may also swarm (Hardy and Gunther, 1935) and occur abundantly

in plankton hauls (Stephensen, 1923 and 1924; Mackintosh, 1934; Hardy and Gunther, 1935; Bigelow, 1926; Kielhorn, 1952; Siegfried, 1965). On repeated occasions, very great quantities of P. gracilipes (Norman, 1909[1]; Brady and Norman, 1909[1]; Ritchie, 1913[2]), P. japonica[3] (Behning, 1939) and P. gaudichaudii (Gray and McHardy, 1967) have been washed ashore.

Aggregation would appear to be characteristic of Parathemisto wherever it is abundant. As pointed out by Stephensen (1924), this feature tends to make the figures on abundance difficult to interpret. When on two occasions[4] swarming of Parathemisto gaudichaudii had been observed off the Yorkshire coast, no unusually large numbers of the species appeared in North Sea collections of the survey (Table 16). Presumably the swarms were restricted in space or time.

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[1] As noted by Stephensen (1924).

[2] Though Ritchie referred to this as Euthemisto compressa, the original material in the Royal Scottish Museum (Reg. No. 1907-79) is recorded as E. compressa (Goës) var. gracilipes Norman and has been identified on reexamination as P. gracilipes (Gray and McHardy, 1967).

[3] Synonomy and distribution (Bowman, 1960) suggests that this may actually be the very closely allied species P. pacifica.

[4] On June and July of 1966 (Gray and McHardy, 1967) and, January of 1967 (Gray, 1967 - personal communication).

G3.2 Feeding relations (including parasitism)

Parathemisto, because of its swarming activity, forms a source of food which can be obtained economically by a variety of large, actively swimming predators. In its pelagic environment this hyperiid forms an important link in the food-chain.

In the Antarctic, Parathemisto gaudichaudii can be a major food of the Sei whale (Nemoto, 1968). It is the preferred crustacean prey of certain sea birds (eg., the penguins Eudyptes chrysocome, E. chrysolophus and Pygoscelis papua; the diving petrel Pelecanoides georgicus; and the prion Pachyptila crassirostris) on Heard Island (Ealey and Chittleborough, 1956) and a food of the fish Notothenia rossi and Chaenichthys rhinocerotis off Kerguelen Island (Hurley, 1960). West of South Africa, this species is often found packed in the stomachs of the maasbanker (Trachurus trachurus) a common fish caught commercially there on a large scale (Siegfried, 1965). Also off this west coast, young Parathemisto form a main part of the diet of salps (Van Zyl, 1960, cited by Siegfried).

In Arctic waters Parathemisto abyssorum is known as a food of the cod (Brown and Cheng, 1946) and P. libellula is eaten by the arctic char (Grainger, 1953), the harp seal (Dunbar, 1941) and the parakeet Auklet (Bédard, 1969). In Ungava Bay, in the Canadian North, hyperiids (probably Parathemisto) often account for a

large proportion of the stomach contents of the arctic guillemot Uria lomvia (Tuck and Squires, 1955). In the North Atlantic and North Sea, pelagic amphipods are eaten by cod (Kashintsev, 1962; Gray and McHardy, 1967 - P. gaudichaudii); herring (Hardy, 1924 - Themisto gracilipes), redfish (Lambert, 1960; Kashintsev, 1962) and long-fin tunny (Le Danois, 1921 - E. bispinosa, cited in Kane, 1966). In the North Pacific Parathemisto (probably P. japonica or P. pacifica) may form a substantial part of the pelagic food of the salmon (Allen and Aron, 1957; Tsurato, 1963), the sardine (Brodsky and Jankovskaya, 1935, cited by Behning, 1939), and the common squid (Soeda, 1956, cited by Okutani, 1962).

During spring and early summer larvae of the redfish Sebastes, the adults of which prey on Parathemisto (Lambert, 1960; Kashintsev, 1962), appear in CPR collections from subarctic water between Iceland and Newfoundland (Henderson, 1961; Fig. 15 of thesis). At this time, however, they feed mainly on small foods such as the gastropod Spiratella and the eggs of Calanus (Einarsson, 1960) and presumably not to any degree upon Parathemisto which, at this time of year, is represented largely by maturing adults and other specimens of relatively large size (Figs. 34 and 36). While Sebastes is thus in the near-surface water, therefore, Parathemisto is unlikely to be an important source of food. Only later, after the majority of larval redfish have descended (Henderson, 1961;

Fig. 15 of thesis), and begun the transition toward feeding on larger organisms such as copepodites, small copepods and even adult euphausiids (Einarsson, 1960), would significant predation on this hyperiid be a possibility.

South and west of Iceland lies a population of the pelagic redfish Sebastes mentella. While the larval fish feed near the surface mainly on the copepod Calanus finmarchicus and the pteropod Spiratella retroversa (Bainbridge and McKay, 1968), the most important food consumed by the adults, living at depth, are hyperiids of the genus Parathemisto (P. abyssorum was very common and P. gaudichaudii common, in the gut; Jones, 1970). Little, if anything, is known of the juveniles of this fish during its period of dietary transition. Here rates of consumption are important, especially in assessing the role of hyperiids as a food source for this stock of potentially commercial value.

Although often the prey of older fish, Parathemisto may be in direct competition for food with the younger fish; P. gracilipes may even feed on them (Williamson, 1950). Parathemisto libellula in the Arctic has been found to ingest a variety of small crustacean plankton including the naupliar and early copepodite stages of Calanus as well as some algal and detrital material (Dunbar, 1946). Similar foods have been found in the midgut of P. pacifica in the North Pacific (Bowman, 1960) and P. gaudichaudii in the western North Atlantic (Bigelow, 1926). Off the west coast of South Africa P. gaudichaudii feeds rather indiscriminately

on everything smaller than itself, its gut contents reflecting the composition of the plankton, with the exception that the juveniles feed on phytoplankton to a greater degree than do adults (Siegfried, 1965). Here the main food items of the older specimens were copepods and to a lesser extent euphausiid larvae and juveniles. This species has been seen (Hardy and Gunther, 1935) to feed on the young of Euphausia superba, the euphausiid upon which fish and many other forms of life in the Antarctic depend. Such competition for food might be an important factor in the survival of young fish, especially during the critical period (Wickstead, 1965) when the yolk is used up and a planktonic diet is required.

Important organisms sampled from subarctic water by the CPR (subarctic water, Table 5) became increasingly available to the surface consumers according to a seasonal succession. Thus, closely following the appearance of larval Sebastes in spring came the adult and young of Calanus, the euphausiids and the general phytoplankton; these were in turn succeeded by the copepod Euchaeta norvegica and the hyperiid Parathemisto gaudichaudii (Fig. 15). Whereas Calanus feeds mainly on phytoplankton (Marshall and Orr, 1955), euphausiids consume both phytoplankton and a variety of zooplankton, and Euchaeta norvegica and Parathemisto gaudichaudii eat primarily animal food (Conover, 1960 and others).

Judging from their known food preference and the seasonal availability of various organisms in the subarctic surface waters, one may speculate on their food relations.

Thus, Calanus adults would at first be living off reserves. Phytoplankton would then bloom and provide food for their further development and for the growth of their offspring. Young euphausiids would devour phytoplankton and probably also the eggs and young of Calanus. The carnivores Euchaeta and Parathemisto which follow would then have available, in addition to the young and later stages of Calanus, the young of euphausiids.

At first, the population of Parathemisto would be mainly composed of adults, possibly capable of attacking larval Sebastes or at least competing with it for food. Later the composition would be primarily of young individuals dependent on smaller food, which could perhaps include some late blooming phytoplankton. At this time Parathemisto might possibly compete with Euchaeta for the remaining young of Calanus.

Although the food organisms available to Parathemisto are suggested here and in the literature, virtually nothing is known about rates of consumption. Data on respiratory requirements, enzyme activity and biochemical composition could give helpful indirect evidence, but knowledge of these aspects is incomplete.

Kane (1964) described a parasite, Thalassomyces marsupii, which attacks the ventral nerve cord of Parathemisto gaudichaudii. In its later developmental stages, this organism forms a root system inside the host and a fruiting body outside (between the pereopods of the amphipod),

characteristics which place it with the Ellobiopsidae, a family of parasites having both protozoan and fungal affinities (Kane, 1964). Thalassomyces marsupii also infects P. abyssorum and some amphipods of the gammarine family Eusiridae; these hosts (including P. gaudichaudii) have in common an actively swimming and voraciously predatory habit (Vader and Kane, 1968).

Infection of Parathemisto by the ellobiopsid Thalassomyces marsupii was discovered on three specimens taken on different occasions from localities of the north-eastern North Atlantic probably within the influence of the North Atlantic Drift current (Fig. 1):

HOST SPECIES	MONTH	YEAR	POSITION[1] °N	°W	NUMBER OF HOSTS
Parathemisto gracilipes	Nov	62	60.5	0.0	1
P. gaudichaudii form compressa	Mar	64	59.5	4.0	1
	Jan	65	58.5	14.0	1

One specimen was of P. gaudichaudii, the species on which the parasite was originally described (Kane, 1964); two were of P. gracilipes, a new host.

The rate of infection may have been higher than is suggested by the occurrence of these few specimens. In its early stages, the parasite does not appear externally and, when in later development it does, it may be hidden between the pereopods of the host, within the brood-pouch

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[1]Position, here, is the approximate centre of the "statistical square" of collection.

region. Except under close examination, this external part -- the fruiting body of the ellobiopsid -- may well resemble eggs within the brood pouch of its host. Vader and Kane (1968), for example, have shown that a sketch and detailed description by Sexton of presumed eggs in the gammarine amphipod Rhachotropis helleri (Fam. Eusiridae) was in fact a very good likeness of the gonomeres of Thalassomyces marsupii. Detection of parasitism may be further reduced by collection damage, in that the visible part of the ellobiopsid might occasionally be broken off and separated from its host.

G3.3 Breeding

Histological studies have shown that females of Parathemisto gracilipes (Evans, 1968b) and P. gaudichaudii (Kane, 1963) may have small eggs in the ovary as well as late eggs or young in the brood pouch. Furthermore females of P. pacifica carrying brood-pouch eggs or young may also be nurturing, within the ovaries, eggs in two stages of development (Bowman, 1960). Although P. abyssorum and P. libellula are believed to breed only once and then die (Bogorov, 1940 and Dunbar, 1957, respectively), there is apparently no histological evidence to suggest that individuals may not spawn repeatedly over an extended period.

In the Barents Sea Parathemisto abyssorum is believed to live for two years before maturing and breeding

once in late winter (Bogorov, 1940). In the Canadian Arctic P. libellula may similarly take about two years to reach maturity when, from summer into winter, females carry eggs (Dunbar, 1957). Both species occurred so rarely in the present survey that evidence with which to assess breeding is lacking.

Bowman (1960) found that mature females of Parathemisto pacifica, collected during three cruises off California and Baja California, were smaller in March and November than in July. Among other hypotheses, concerning temperature during development and seasonal change in vertical distribution, he suggested that those females breeding in July were older and larger members of the generation sampled in March and that the November population must be of a new generation.

Abundance of Parathemisto pacifica increased from March to July and decreased to a low in November (Bowman, 1960). In all probability the major cause of the increase was production of a new generation. Whereas some of this generation would mature by autumn of the same year (this species matures at a small size), most would attain adulthood by the following year, breeding in spring and summer and dying before autumn. Conceivably the life-cycle might approximate one year, with a generation breeding in autumn of the first year as well as in spring and summer of the second.

Stephensen (1924) found no evidence of Parathemisto gracilipes (as Themisto gracilipes) population the middle region of the North Sea, and noted that this agreed with the

suggestion of Brady and Norman that the species was carried into the North Sea and along the northern part of the British east coast, by a current from the north. Marshall (1948) proposed, further, that the species did not propagate within the North Sea. Vane (MS1951), however, showed that the central part of the North Sea could support a viable breeding population but conceded that the north-east part could well contain specimens from Atlantic populations.

In the North Sea a generation of Parathemisto gracilipes may live at least one year and in this time breed during two seasons before dying (Evans, 1968b). Evans established, from nearly two years of regular collection at 25 m of depth off the Northumberland coast of England, that there are large adults which attain breeding condition in March and April and small ones which reach this state in August and September. After breeding from late summer to early autumn, many of the small adults apparently revert to an immature condition, overwinter, and mature a second time in the spring -- at a larger size. Young released in spring are believed to mature quickly and breed in the same year, whereas those released from late summer to early autumn would have to overwinter and wait until the succeeding summer for maturity.

Though this seasonal cycle of size and maturity was consistent for two years running, Evans (1968b) was unable

to associate it with changes of abundance[1]. On the other hand the seasonal maximum of the species in the central North Sea, which occurs at the 10-m level in late autumn and early winter, was found by Vane (MS1951) to be composed of juveniles. Marshall (1948) also found that the greatest abundance took place in autumn and winter.

The north-westerly quarter of the North Sea investigated in the present survey (C2) includes the station sampled by Evans (1968b). In this region, variability in abundance was greater between years than between months. As with the findings of Evans, the year 1964 was richer than 1965. A similar annual fluctuation found off the west of the British Isles suggests that the success of breeding of hyperiids is influenced to some degree by the presence of a common factor. The flow of water from the North Atlantic Drift, which is known not only to wash the western shores of the British Isles but also to penetrate along the eastern coast, might possibly have contributed to the coincidental increase of hyperiids in these two regions.

Hyperiids in other parts of the remaining North Sea varied noticeably in abundance both seasonally and annually but in accordance with no common trend. Populations in the north-east, south-west and south-east each demonstrated

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[1] An affinity of juveniles for the surface and a tendency for adults to move through various depths might account for this discrepancy observed at the 25-m level (for further discussion, see section G4.2).

individual patterns of fluctuation, none resembling other patterns, either inside or outside of the North Sea. In these basically neritic areas Parathemisto gracilipes would most likely be dependent for the success of its spawn on a variable renewal and retention of Atlantic admixture.

Except possibly in mid-winter, mature specimens of Parathemisto gaudichaudii in the southern hemisphere may be present year round, whether from the Southern Ocean (Kane, 1966) or from upwelling water off the west of South Africa (Siegfried, 1965). They were in highest proportion during late winter and early spring in the Southern Ocean (Kane, 1966 - Table 12) whereas, off South Africa, ovigerous females were relatively abundant mainly in spring but also in late summer and early autumn (Siegfried, 1965 - Fig. 7). In the Southern Ocean, young were very abundant in early summer and moderately numerous in autumn (Kane, 1966 - Fig. 11) while in upwelling waters off South Africa their peak abundance varied annually from early to late summer (Siegfried, 1965 - Fig. 6).

Siegfried (1965) and Kane (1966) found immature individuals which were larger than mature ones and considered that these might have reverted to the immature morphology after having spawned. Siegfried, however, discounted this possibility in favour of another involving the effect on growth of environmental factors (eg., temperature and food).

In the western North Atlantic in the Gulf of Maine,

young of this species[1] occurred during all months from February to October and breeding was greatest in summer (Bigelow, 1926). In the north-eastern North Atlantic between Iceland and the British Isles, juveniles were present over a similarly extended but later part of the year (April to December) and maximal from late summer, when adults were most abundant, to mid-autumn (Vane, MS1951). In the North Atlantic, south-west of Britain, where the species is believed to be at the southern limit of its range, breeding was less in summer than in spring and autumn (Stephensen, 1924 - p 106 and 1925 - p 236). Stephensen (1924) showed that whereas the proportion of adult females which carried eggs was 27-30% in March and September, it was only 3-4% in June. In this region, adults of both sexes attained sexual maturity at different sizes depending on season. In March they were either small or very large in size, in June they were medium and in September moderately large (Stephensen, 1924). Stephensen suggested that among the adults of spring, the small ones were born in the previous autumn and the large ones in the previous spring.

These observations of Stephensen on Parathemisto gaudichaudii may be interpreted further, considering the forementioned findings of Evans (1968b) for P. gracilipes.

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[1]Where both this species and Parathemisto gracilipes were found in shelf waters south-east of New York, however, abundance was greatest in early winter, though also high in mid-summer (Grice and Hart, 1962 - Appendix Table 2).

Of the small adults, a few could have bred in spring, then passed the summer in immature condition to mature and breed in autumn, at the moderately large size; these could then over-winter (perhaps once more in the immature stage) and breed again in the spring, as the very large adults that appear alongside those small mature specimens of the next generation. Thus it is possible that specimens born in the warm season of one year could spawn twice (spring and autumn) in the succeeding year and then, a third time (spring) in the year next again.

The present investigation shows, among specimens in the surface water, a succession of size and maturity which may be related to breeding and other processes. This seasonal succession varied geographically. To discuss the involvement of this succession with the factors of the environment, the evidence -- often fragmented in the "Results" due to the variety of methods by which it was gleaned -- is here reorganized into a unified interpretation.

Although a number of young of Parathemisto gaudichaudii appeared in surface water of the subarctic gyre firstly in spring, the bulk of them did not show until summer and early autumn (Figs. 34 and 36). Mature or maturing animals, on the other hand, increased numerically mainly from spring to summer and then virtually disappeared from the surface waters by early autumn. The larger specimens, which entered the surface waters during summer are believed to have been among those which gave birth to the numerous

young which followed. Most adults left the surface by early autumn and most young descended by late autumn.

As shown for 1965, appearance of the species at the 10-m level was mainly confined in winter to that part of the Labrador Current which extends southward alongside the American coast (Figs. 36-41). Though young specimens were present only here in winter, early spring brought them into those surface waters further north (Fig. 37). By summer these and all other stages of growth and maturity had become distributed widely over subarctic and North Atlantic Drift waters (this was true also for 1962-4, Figs. 42-46). With late autumn, the presence of young in the surface was again confined to southerly regions but this time were found in the Atlantic Drift as well as the Labrador Current (Fig. 37).

The seasonal increase in abundance began three months earlier in the west than in the north and north-east of the North Atlantic (Fig. 22). This accords with the comparison (above) of the breeding times given by Bigelow (1926) and Vane (MS1951), and reflects the earlier appearance of young in the southerly extreme of the Labrador Current (Fig. 37). Einarsson (1945) similarly found in the North Atlantic that euphausiids generally begin spawning later the further north the breeding area is situated. He indicates that temperature is not the controlling factor, but considered that spawning might be somehow timed to correspond with the blooming of phytoplankton.

Length of day, time of seasonal warming and temperature were considered as agents which, during winter and spring, might have determined the time for breeding. Day-length, with its latitudinal variations, seems the most likely of these, even though in one north-easterly area of intermediate latitude (C5), the main seasonal increase in abundance appeared slightly later[1] than would have been expected (Fig. 22; sequence in Table 9). Dunbar (1957, p 817) suggested that light or some other factor is more likely than temperature to stimulate gonadal maturation of Parathemisto libellula.

In surface waters of the North Atlantic Drift off the west of the British Isles, Parathemisto exhibited double peaks of abundance. Specimens in the north of this region (area C5) became fewer in July while those in the south (D5) were less plentiful from July to September (Fig. 22). As mentioned earlier, Stephensen (1925) suggested that south of Britain in the eastern North Atlantic P. gaudichaudii is in the southern extreme of its range with regard to temperature and therefore fails to breed in the summer because of the heat. Although the region west of the British Isles is not quite so far south as the area

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[1]This delay might have been caused by high temperatures in mid-summer having inhibited reproduction (Stephensen, 1925; see discussion in paragraphs ahead).

studied by Stephensen (1924), the seasonal variation in abundance tends to have reflected similarly this mid-summer reduction in population growth. Summer warming would appear also to delay sexual development of the copepod Calanus glacialis where it inhabits the White Sea (Prygunkova, 1968), and to suppress the release of sexual products in the ascidian Dendrodoa grossularia living on the Essex shores of the southern North Sea (Millar, 1954).

Where the population size was reduced during July, August and September, the sea-surface temperatures averaged above 13° C for those three months (Fig. 22). Other studies of distribution have suggested upper limits of temperature for the species. Bigelow (1926) indicated that in the Gulf of Maine the species prefers temperatures below 14° C, with an optimum below 12° C for adults. Whiteley (1948) considered that around Georges Bank temperatures above 15° C were unfavourable. Siegfried (1965) showed, in charts of distribution off the west of South Africa, that occurrences down to 100 m were few where temperature at 30 m depth was 17° C or above. The present study also suggests an upper limit of temperature. At or above 13° C the number of specimens was reduced. Provided that abundance reflects reproduction, this reduction may suggest inhibition to breeding. Stephensen (1925) suggested that such might have occurred south of the British Isles; the present information indicates that it may also have taken place in an adjacent area west of these islands.

During the months of summer and autumn Parathemisto gaudichaudii became widely dispersed and entered both warm Gulf Stream and North Atlantic Drift waters and cold Arctic waters (Fig. 17b). These extensions of the distribution, however, were not particularly viable. At the extremes of dispersal, for example off Greenland, Iceland and the north-west of Britain, the composition was mainly of larger specimens with fewer young than were found in surface waters of the subarctic mass (Table 12). Even within the subarctic water, where most young specimens were found, the success of breeding appears to have differed geographically. Parathemisto in the west had a higher number and percentage of developing young than had populations in the north and east (Fig. 30, cf. b and c; Fig. 33, cf. B6 and D8). This higher productivity may well be related to the earlier start and more extended period of breeding in the west (Figs. 22, 34, 36, 37 and 42).

G4 Distribution of Parathemisto

G4.1 Horizontal distributions of Parathemisto

Bowman (1960) examined the world distributions of known species of Parathemisto and confirmed that the genus is essentially epipelagic, overwhelmingly dominating the abundant amphipod fauna of cool surface waters.

Parathemisto libellula is circumpolar in the Arctic Ocean and penetrates, probably with Arctic water (Dunbar, 1964), into the North Atlantic and North Pacific (Bowman, 1960).

Parathemisto abyssorum is found throughout the Arctic into the subarctic Atlantic (Stephensen, 1923). Ekman (1953) consideres it primarily Arctic but penetrating southwardly in deeper water. Dunbar (1964) suggests that it is a "subarctic" species; that is, living primarily in water which is basically Arctic in origin, but with traces of Atlantic admixture.

Parathemisto pacifica abounds mainly in subarctic water of the Pacific (as defined by Sverdrup et al., 1942) and is not known to penetrate into the Arctic (Bowman, 1960).

Parathemisto gaudichaudii is circumpolar in subantarctic and West Wind Drift waters of the southern hemisphere (Kane, 1966) and, in the northern Hemisphere, is wide spread from Arctic to temperate waters of the North Atlantic (Stephensen, 1923 and 1924).

Parathemisto japonica inhabits cold subarctic water mainly within the confines of the Sea of Japan and the Sea of Okhotsk in the western North Pacific, usually in the absence of P. pacifica (Bowman, 1960).

Parathemisto australis occurs off south-west Australia and New Zealand, in coastal waters associated with deep subantarctic water or warm surface-water (Hurley, 1955;

Bary, 1959).

Parathemisto gracilipes is similarly restricted to neritic conditions but is more widely known than P. australis, being reported in the northern hemisphere from the western North Atlantic (Grice and Hart, 1962), eastern North Atlantic, North Sea and Mediterranean (Stephensen, 1924), the Yellow and East China Seas (Bowman, 1960), and the Bay of Bengal (Tsuruta, 1963), and in the southern hemisphere from the vicinities of New Zealand (Hurley, 1955), the Juan Fernandez Islands (west of Chile; Bowman, 1960), Tristan da Cunha (Stephensen, 1949 - query on identification) and the South Sandwich Islands (Barnard, 1930 - p 421). From its distribution in the eastern North Atlantic (Stephensen, 1924) and its T-S relationship off New Zealand (Bary, 1959), it appears that this species may inhabit waters which are warmer than would be preferred by P. gaudichaudii.

From their world distributions Parathemisto libellula and P. abyssorum would seem usually to inhabit waters of mainly Arctic origin, but occasionally to penetrate into subarctic water of more pronounced Atlantic admixture. The few specimens taken in the present survey were either on the edge of distributions shown by Bowman (1960) and Dunbar (1964) or marginally outside these. Their positions of collection quite probably indicate a proximity with water of Arctic origin but, because relatively more samples were examined for some of the months and areas at which these species were collected, the occurrences (Table 11) do not

necessarily reflect typical geographical or seasonal distributions.

Bowman (1960) suggested that Parathemisto gracilipes was absent from the Atlantic coast of the United States because of the limited availability there of water amenable in temperature. He later helped identify this species, however, from collections made between New York and Bermuda (Grice and Hart, 1962). Grice and Hart (1962) classified it, along with P. gaudichaudii, as an inhabitant of cold neritic and shelf water in contrast to plankton of warm slope and Sargasso Sea water.

Most collections of Parathemisto gracilipes have been from the Mediterranean Sea, the Atlantic coasts of Ireland, Spain and Portugal, the east coast of Britain and the southern North Sea (Tesch, 1911 and 1915; Stephensen, 1924; Southward, 1963; Verwey, 1964 - p 304). This has left the impression either that the species is absent from the middle region of the North Sea (Stephensen, 1924) or that, if present, it is merely a recruit from Atlantic coastal waters (Marshall, 1948). Nevertheless Vane (1951 - MSc thesis) showed that the central North Sea may support a moderately large breeding population. As his work is unpublished, however, the generally known distribution of P. gracilipes in the North Sea remains incomplete (Evans, 1968b).

Kunne (1937) showed that within the southern North Sea, the species (as Themisto abyssorum; see Marshall, 1948 -

footnote) was consistently most numerous in the north-west and occasionally present in the extreme south-west (die Hoofden). He suggested that specimens in these regions came in association with water from the high seas, from the north and via the English Channel, from the west. Parathemisto gracilipes is now recognized to be indicative of mixed oceanic and coastal waters whether in the northern North Sea (Fraser, 1961) or in the vicinity of the Channel (Russell, 1939; Southward, 1961-3).

Marshall (1948) has shown Parathemisto to be widely distributed in central and north-western parts of the North Sea. Vane (MS1951) confirmed the species to be P. gracilipes and showed the centralized population at least, to be endemic. He conceded, however, that summer increases in the extreme north-west may have been due to specimens carried there by currents from the Atlantic. The greatest abundance and geographical dispersal of the species may generally appear in winter and spring (Marshall, 1948; Vane, MS1951) though in a local area, such as off Northumberland (Evans, 1968), the same seasonal pattern may not be repeated from one year to the next.

Within near-surface waters explored by the present survey Parathemisto gracilipes occurred most commonly in the northern North Sea (north of 55° N). Generally in winter and spring the distribution remained within this region whereas in summer and autumn it occupied as well as a greater part of the North Sea, also the Atlantic coasts of

France and the British Isles (Fig. 32).

The geographical position and extent of the North Sea population varied considerably, depending on the seasons and years involved (Fig. 18). Whereas in 1962 and 1963 it remained mainly in the northern North Sea, being spread from west to east in winter-spring and confined to the east in summer-autumn, it stayed primarily in the west in 1964 and 1965, being restricted to the north in winter and spring but extending into the south during summer and autumn.

This latter distribution which stretched along the British coast south to the Dogger Swirl (Fig. 18d) is of a geographical pattern very similar to that described by Russell(1939) for the occurrence of mixed oceanic and coastal water during a strong Atlantic inflow from the north. Since Parathemisto gracilipes is included as a plankton indicator of this mixed water (Russell, 1939; Fraser, 1961; Southward, 1961-3), the various shapes of its distribution in the North Sea (Fig. 18) probably reflect the extent of this water, as it may have been influenced by the variable strength, direction and quality of inflow from the Atlantic. Although increased salinity in summer may be a regular feature indicating Atlantic inflow along the English coast, such consistency is not the rule in the central North Sea where mixed water shifts from place to place, more than other types of water, depending on the interaction of several components and on the circulation (Böhnecke, 1926).

The abundance of hyperiids in the eastern North Atlantic varied perhaps more between years than between months (Table 8). In the north-western quarter of the North Sea (area C2) and in a region of the North Atlantic Drift (including C5 and D5), specimens were especially abundant during the year 1964 while in other areas, annual variations were either unimportant or not interrelated. Possibly environmental conditions experienced by hyperiids in the North Atlantic Drift and by Parathemisto gracilipes in the north-western North Sea were similar, perhaps by virtue of a common source.

In his account of the Danish collections by THOR and INGOLF, Stephensen (1923 and 1924) summarized the known distribution of Parathemisto gaudichaudii (as Themisto compressa) in the North Atlantic. The species was found mainly in the West Greenland Current, Irminger Sea, Labrador Current and North Atlantic Drift (Vosseler's Gulf Stream station) but appeared occasionally at isolated locations at the beginning of the Gulf Stream (Vosseler's Florida Current station) and in the Sargasso Sea (deep haul, 0-400 m; possibly from deep subarctic water?) and, exceptionally from Arctic waters (Stephensen, 1923) and from the North Sea (identifications often considered doubtful by Stephensen, 1923).

Further investigations in the western North Atlantic, particularly in the Gulf of Maine (Bigelow, 1926), the Bay of Fundy (Fish and Johnson, 1937), between Cape Cod

and Chesapeake Bay (Bigelow and Sears, 1939), over Georges Bank (Whiteley, 1948), in and about Belle Isle Strait (Bousfield, 1951) and between New York and Bermuda (Grice and Hart, 1962), filled gaps in the distribution as known by Stephensen. This assisted Bowman (1960) to chart a generalized world distribution for the species and Dunbar (1964) to revise and extend the known Arctic and North Atlantic occurrences (further enlarged in an MSc thesis by Shen, 1966). Following her investigation of the DISCOVERY collections from the Antarctic, Kane (1966) updated the world distribution and in so doing modified it somewhat from that of Bowman (1960), particularly by extending the boundaries for dispersal in the Southern Ocean and within the eastern North Atlantic.

In the present survey this cold-water oceanic species was positively identified from nearly all 38 areas for which samples were examined. It was not recognized in samples from the south-eastern North Sea nor from southerly extremes of the central and eastern North Atlantic. This is not surprising since the south-eastern North Sea characteristically maintains a neritic plankton (Russell, 1939) and the south-eastern North Atlantic carries, in southerly swirls of the Drift, water of nearly pure Gulf Stream origin (Sverdrup et al., 1942; also Fig. 1). Though the survey confirms that the species is neither neritic nor warm-water in its affinities, the full extent of dispersal into the North Atlantic Drift water to the south

is not yet known. The frequent appearance of specimens north-east of the Grand Newfoundland Banks (Figs. 30b, 31, 37-46) would suggest that southerly dispersal of the species in oceanic water may extend further than shown in the present or previous investigations. Recently the CPR survey has been extended to cover part of the region in question. Analysis of the resulting samples might provide some of the missing information.

Although Dunbar (1964) and Siegfried (1965) each named the subarctic water-mass as the main home for Parathemisto gaudichaudii in the North Atlantic, the literature provides little quantitative comparison, beyond that of Stephensen (1923, 1924), to verify this. Bowman (1960), Dunbar (1964) and Kane (1966) though giving excellent revisions of the extent of distribution were not able to elaborate on geographical variations in abundance over the North Atlantic.

Siegfried (1965) showed that off the west coast of South Africa, Parathemisto gaudichaudii lived near shore in cool water upwelled from the depths. Although its range extended into warmer water off shore and to the south, specimens there were fewer. Kane (1966) demonstrated that abundance of the species varies latitudinally in the Antarctic. Though it ranged across the Antarctic Convergence from the northern boundary of subantarctic water (at the Subtropical Convergence) to the southern limit of the West Wind Drift, this hyperiid was abundant only along belts on

either side of the Antarctic Convergence; at the Convergence itself and towards the northern and southern edges of distribution, specimens were fewer. The maxima north and south were maintained throughout the year except in late autumn and winter when the population to the north decreased and that to the south became displaced nearer the Convergence. Kane considered a few possible explanations for the paucity at the Convergence and for the seasonal shift of abundance, but found them unconvincing.

Bigelow and Sears (Bigelow, 1917 and 1926; Bigelow and Sears, 1939) found that the species (as Euthemisto compressa and E. bispinosa), though not always abundant, was a characteristic member of waters over the American shelf from Chesapeake Bay to Nova Scotia. From comparisons of seasonal differences in abundance over a period of years, they suggested that the centre of population shifts northward as the summer advances and returns south as autumn commences, as would be expected for a boreal species influenced by summer warming.

Within the geographical range of surface waters surveyed in the present study, Parathemisto gaudichaudii was most abundant in subarctic water (cf. Figs. 1 and 30b). The species was most frequently present at two centres (Fig. 17) corresponding roughtly with regions where warm water from the Gulf Stream system could override and mix with cold water of the subarctic mass. There is a meander of the Gulf Stream current (or a branch of the North

Atlantic Drift as interpreted in Sverdrup et al., 1942) which loops northward from a position just east of the Grand Banks of Newfoundland and, a branch of the North Atlantic Drift which turns west, south of Iceland (Fig. 1). In these regions specimens were present at the surface nearly every month for four years. Conceivably conditions provided through mixing of warm and cold waters here, encouraged the seasonal presence of the species to be so extended.

In surface water outside the subarctic mass, incidence of Parathemisto gaudichaudii appears to have been more variable. Generally occurrences became much more prevalent in the summer and autumn than in the winter and spring and, at this time, extended north and south beyond subarctic water. These summer-autumn projections of distribution, however, were not consistent over the years and appeared rather less widely over 1962-3 than during 1964-5. Bigelow and Sears (1939) found that, from year to year, abundance over the American continental shelf was comparatively constant during winter and spring but varied widely in summer.

Over the shoal areas of the Grand Newfoundland Bank and the European continental shelf, incidence in summer and autumn was rather lower than might have been otherwise expected (Figs. 17 and 18), and as well, numbers were generally fewer (Fig. 30, b and c). Similarly around Georges Bank to the south, Whiteley (1948) found the species

abundant over deeper water but rare in shoal areas of the bank.

In the North Sea proper, where Parathemisto gracilipes is endemic, specimens recognizable as P. gaudichaudii occurred only intermittently and at scattered locations throughout the present survey. This is perhaps surprising since the species 1) is larger and therefore may be more readily identified, 2) was numerous in the summer and autumn north of Scotland (Fig. 31), 3) was swarming and breeding off the Yorkshire coast of England in June, 1966 (Gray and McHardy, 1967), and 4) formed four-fifths of a similar swarming, of which the remainder was P. gracilipes[1], in January, 1967 (Gray, 1967, personal communication). Apparently the offspring of P. gaudichaudii whose parents did penetrate into the North Sea either dwindled in numbers or lost their identity.

In certain regions, namely off the west of Spain and in the English Channel, incidence of Parathemisto remained extremely low over the four years, despite summer-autumn invasions elsewhere. Off Spain, the Gulf-Stream influence may have been dominant and the temperature too high. In the English Channel, the resident "Channel Water", which has been more or less continuously poor in plankton since September of 1931 (Russell, 1939; Southward, 1962-3), quite possibly is unsuitable for this hyperiid.

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[1] An earlier swarming off the Yorkshire coast (Ritchie, 1913) consisted entirely of Parathemisto gracilipes (Gray and McHardy, 1967).

The present information suggests that Parathemisto gaudichaudii lives best where subarctic water overlies oceanic depths but, nevertheless, is an adaptable species able to invade new territories, with the occasional risk of succumbing to hostile conditions. Dunbar (1968) has suggested that the genus Parathemisto, like many other organisms inhabiting cooler marine environments, is still in a pliable state of evolution. He further speculated (Dunbar, MS1969) that in such a position, an organism may be more adaptable than one which has matured in a more stable environment, such as the tropical ocean may offer.

Although the bispinosa and compressa forms of Parathemisto gaudichaudii have similar distributions (Stephensen, 1923 and 1924), their relative abundance may differ depending on the season and the region. In the Southern Ocean where water masses lie in belts more or less parallel to lines of latitude, the bispinosa form is found to increase proportionately toward higher latitudes (Barnard, 1932; Kane, 1966). The compressa form does not decrease in numbers, however, to compensate for the progressive ascendancy of the bispinosa form (Kane, 1966). Presumably instead, it is those specimens of intermediate form which become less numerous poleward.

The change toward more bispinosa did not accelerate near the approximate position of the Antarctic Convergence (cf. Figs. 5 and 9 of Kane, 1966). Rather it was a gradual one, more likely to be associated with parameters which might alter progressively with latitude (eg. day-length)

than with properties distinctive to water masses, which would meet rather abruptly at a boundary (eg. the Convergence).

Bigelow (1917 and 1926) and Bousfield (1951) found that in shelf waters of the western North Atlantic, between the Gulf of Maine and Labrador, compressa usually predominated in open neritic conditions while bispinosa was relatively more common in waters further to sea. Bigelow (1917 and 1926) indicates that bispinosa was most abundant in summer. Kielhorn (1952) suggested that in these waters the two forms show slightly different centres of seasonal abundance.

Vane (MS1951) showed that in surface waters of the eastern North Atlantic between Iceland and the British Isles, compressa may be the most numerous form in spring and early summer, but bispinosa can become overwhelmingly predominant in late summer. Stephensen (1924) indicated that on average bispinosa could be the more abundant form in warm surface waters south of Britain (compare his tables of pp 106 and 108). Here both forms, of the female at least, appear to have been more numerous in spring than in summer and autumn (Stephensen, 1924 - pp 106 and 109).

Shen (MS1966) found that bispinosa is the common form off Georges Bank but the least abundant in the Canadian North, where compressa is generally dominant and penetrates to higher latitudes (69° N) than does bispinosa (62.5° N). This relationship to latitude is quite the opposite to that

found between compressa and bispinosa in the Southern Ocean (Barnard, 1932 and Kane, 1966; see above discussion) and might suggest that, between hemispheres, poleward changes in environment or physiology may take independent courses.

In the present survey the relative abundance of the two forms is shown to change not only seasonally and geographically but also annually. In 1962 numbers were low and the distribution of the bispinosa form was poorly defined. From 1963 to 1965, however, the species increased and the geographical preferences of this form became clear, particularly in summer and autumn. While compressa was most prevalent in the north-western North Atlantic, bispinosa dominated in the north-east. This dominance suggests that bispinosa perhaps receives benefit from a measure of Gulf Stream water while compressa may gain similar advantage from a portion of Arctic admixture. Though it bears no relationship to the apparently opposite situation found in the Antarctic (Barnard, 1932; Kane, 1966; see discussion above), this hypothesis perhaps explains distributions in the North Atlantic.

G4.2 Vertical distributions of Parathemisto

In the North Atlantic, Parathemisto abyssorum, though numerous in surface waters (above 300 mw) and therefore not a truly deep-sea species, has nevertheless an affinity for greater depths (Stephensen, 1925). Bousfield

(1951) compared numbers at 25 m and the surface in the region of Belle Isle Strait and found the species to avoid the shallower water, especially during the day. Similarly in the southern Norwegian Sea the species occurred more frequently at 35-40 m than at 2-3 m (Hansen, 1960).

In the Canadian Arctic, Parathemisto libellula in its young and immature stages of growth may frequently be collected by net hauls; whereas, mature adults are seldom taken except in the stomachs of seals (Dunbar, 1957). Dunbar (1957) suggested that these adults, if not avoiding the nets, possibly maintain a lower level than other stages. Here and in the Belle Isle Strait region this species tends to occur at the surface in greater numbers during the day than at night (Dunbar, 1957; Bousfield, 1951).

Both species occurred rarely in the present survey, perhaps because they generally occupied greater depths (or more northerly waters) than were sampled. In the few areas from which specimens were taken, more samples than usual had been examined. If this bias were not considered to prejudice the results unduly, one might conclude that these regions were visited not infrequently by water of Arctic origin, either through horizontal transport or upwelling.

Bowman (1960) discovered that during March and November, off California and Baja California, Parathemisto pacifica in the upper 70 m was considerably more abundant at night than by day. On the other hand, in July this

diurnal difference was hardly noticeable. He suggested, among other things, that in March and November some of the population moved twice daily across the 70-m level but in July, all of it remained above this depth.

Living as a rule in neritic regions (Bary, 1959), Parathemisto gracilipes must be considered a species of shallow, rather than deep-sea, waters (Stephensen, 1924). Gray[1] (personal communication, 1968) witnessed that in the North Sea the species may occur more abundantly at the bottom (10-12 m) than at the surface. Stephensen (1924 - p 101) found that in the eastern North Atlantic, though the species was common in the upper 100 m and abundant above 25 m, it often reached depths of 94-180 m and once exceeded about 330 m.

From the present survey Parathemisto gracilipes would appear to occur more abundantly and over a greater part of the year in surface waters of the North Sea than in those along the Atlantic coast of Europe. Although possibly due to reduced breeding, this paucity in the Atlantic might also be related to the specimens tending to seek greater depths, as they appear to have south of Britain (Stephensen, 1924).

Although living room for Parathemisto gracilipes in the western North Atlantic had once been considered insufficient (Bowman, 1960), several representatives of the

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[1] J.S. Gray, Robin Hood's Bay, Yorkshire.

species have since been found there (Grice and Hart, 1962 - identified with Bowman's assistance; also section F4.1 of present study). Whether or not the amount of environment amenable to this species is in fact adequate to sustain a viable population, the questions remain: Where is the source of these or the original specimens? What is the means of their transport?

Though conceivably specimens in the western North Atlantic might originate by environmental modification of the prevailing species, P. gaudichaudii, they are more likely to have been carried there by ocean currents from established populations of the North Atlantic, namely those known in the Mediterranean, North Sea and adjacent regions of the European continental shelf.

The following hypothesis suggests a means of cross-ocean transport which requires that some members of the species undergo rather extensive changes in vertical distribution. While the surface currents connecting the two regions travel generally from west to east and would not provide the transport required, the Mediterranean Intermediate water, flowing from east to west beneath the surface, may assist. A branch of this Intermediate water, after turning northward at its outflow from the Mediterranean, bends westwardly south of the British Isles to flow south-westward across to the American shelf (Sverdrup et al., 1942 - Fig. 188). Here it turns northward and passes under the very surface water in which specimens of P. gracilipes

were discovered.

If specimens in the east were to descend into the Mediterranean Intermediate Water and those reaching the west were to ascend into surface water, the requirements for trans-ocean conveyance of the species would be met. As shown by Stephensen (1924) for specimens south of Britain, the species may occur from the surface to depths exceeding 300 m. Although some specimens might rise to the surface anywhere along the route of the Intermediate Water, their changes for survival might not be as good as those which migrate into surface waters having those warm-neritic conditions such as are available over most of the European continental shelf and in a limited region over the American shelf.

Jaschnov (1961) has indicated that Mediterranean Intermediate Water is the vehicle for dissemination of the copepod Calanus helgolandicus into the North Atlantic where, following its ontogenetic rise to surface levels, it becomes dispersed toward the European coast. Though the species breeds in these surface waters, he believes that the population here is not self-sustaining but dependent upon recruitment from the Mediterranean Sea. The pattern of distribution of C. helgolandicus, which broadly overlaps that of Parathemisto gracilipes, is centred further south than the hyperiid, especially in the North Sea (cf. Figs. 10b and 30a).

In the North Sea, off Robin Hood's Bay, Yorkshire, in February of 1968, actively breeding specimens were

numerous in plankton at the bottom (10-12 m) but few occurred at the surface (Gray, J.S. - personal communication, 1968). Gray, in an earlier personal communication (1966), suggested that swarming in this species is a reproductive phase and occurs only at certain times, on the bottom, while the rest of the time specimens are dispersed in the plankton.

Evans (1968b) found that, though the reproductive events of Parathemisto gracilipes off the Northumberland coast were seasonally consistent, fluctuations in abundance bore them little apparent relationship. Since his collection depth was 25 m, in water extending to 40 m at the bottom, there was room here for vertical changes in the distribution of the population across the level sampled. Conceivably such vertical migration could account for the observed irregularities in abundance.

The present survey, being limited to the 10-m level, could not provide direct evidence on vertical distribution. If, however, the reproductive cycles were seasonally regular, as indicated by Evans (1968b), then that portion of the monthly variability in abundance which was inexplicable and inconsistent between areas and years might, in part, be attributed to local changes in vertical distribution.

Parathemisto gracilipes is one of several zooplankton species which dwell in deeper water by day and occuppy surface waters at night (Russell, 1925). Specimens from along the Atlantic coast south of Britain (Stephensen, 1924)

and in the English Channel off Plymouth (Russell, 1925), are found in abundance near the surface at night though they occur mainly below 20-25 m by day.

The present investigation showed that in all areas inhabited by Parathemisto gracilipes (Fig. 28), specimens were more abundant in surface waters at night than by day (Fig. 19). This diurnal difference in numbers was stronger in the western and northern regions of the North Sea than in the south-eastern North Sea or off the west coasts of the British Isles and France (Fig. 20). Perhaps those Atlantic waters which enter the western and northern parts of the North Sea encourage, by natural selection, a greater diurnal vertical migration than do other waters, of decidedly neritic or Gulf Stream origins.

Stephensen (1925), in dividing surface-water and deep-sea hyperiids of the North Atlantic between those living mainly above and below 300 mw (metres of wire out), classified Parathemisto gaudichaudii as a surface dweller. Nevertheless he found that the species could be taken from depths greater than 1000 m, the bispinosa form less often than the compressa one (Stephensen, 1924).

Bigelow (1917) found that, along the coast of North America between Cape Cod and Halifax, the relative abundance of the two forms differed with depth. Where numbers were large, the ratio of bispinosa to compressa was greater in deep than in shallow hauls. He also discovered that in the Gulf of Maine, the ratio of young to adults was higher near

the surface than at depth (Bigelow, 1926).

The present survey revealed that specimens of small to medium size occurred more commonly in the west than in the north and east of the North Atlantic (Figs. 30c, 31, 33-B6 & D8, 38 and 43). Although the region may provide an environment for more successful breeding and better survival of young, it may also encourage these developing specimens to maintain a shallower vertical distribution than elsewhere.

Form compressa often outnumbered bispinosa in surface waters of the western North Atlantic during August and September and, at least in one year, through to November (Figs. 40, 41, 45 and 46). Differences in vertical distribution between the two forms may account for the dissimilarity in their relative abundance at the surface. Thus in the north-west, where chiefly compressa was being sampled near the surface, bispinosa beneath may have been relatively more numerous, as this form was demonstrated to be in deep hauls, taken between Cape Cod and Halifax (Bigelow, 1917). Conversely in the eastern North Atlantic, though bispinosa predominated at the surface (Figs. 40, 41, 45 and 46), compressa might have been more abundant below.

Mackintosh (1937) found that the vertical distribution of Parathemisto gaudichaudii in the Antarctic showed no noticeable seasonal change across the 250-m level. Siegfried (1965) sampling to a depth of 100 m off the west of South Africa, found that adults (specimens 7 mm or longer) of P. gaudichaudii disappeared in autumn not to

reappear, while young, though decreasing in numbers, overwintered and grew to maturity by the following spring. Kane (1966), also sampling to 100 m but in the Southern Ocean, similarly discovered that mature adults became markedly fewer in late summer and nearly absent in autumn and winter. She suggested that the majority of these either migrated to depths greater than 100 m or died; some, she conceded, would breed in autumn while a few surviving over winter (as the unusually large animals taken occasionally) might spawn again in the spring.

It might be suggested that geographical differences at the 10-m level may be associated with variations in vertical distribution. The high numbers off Labrador might have represented a concentration in near-surface waters whereas the lesser abundance elsewhere could have related to animals having gathered at greater depths. Nevertheless, a distribution similar to that shown in the present study was shown by Stephensen (1923 and 1924) from material taken through a much larger part of the water column. Perhaps the only likely discrepancy might occur south of subarctic surface waters where Parathemisto was obtained in the Sargasso Sea from deep hauls. It is here that Einarsson (1945) found the distribution of Thysanoessa longicaudata to deepen where water of subarctic origin becomes submerged under the warmer Atlantic surface layer. Any similar southward extension of occurrences of Parathemisto gaudichaudii would remain undetected by near-surface sampling such as is carried out by the CPR survey.

Variations related to birth and death, on the other hand, can sometimes be distinguished from those associated with vertical movements in distribution. Whereas in early summer a good part of the increase at 10 m was attributable to immigration of mature or maturing specimens from below, a major portion of the maximum in late summer and early autumn was due to birth of numerous young (Figs. 34 and 36). While adults were fewer in early autumn and their offspring became less numerous by late autumn, a fair number reappeared in spring and summer as maturing specimens, perhaps despite a high mortality (Fig. 33, overall). Except for a few which occurred in the more southerly surface waters over winter, most of these must have remained below the 10-m level. Presumably specimens which overwintered in the North Atlantic, like those in the southern oceans (Siegfried, 1965; Kane, 1966), were mainly immature and, though not generally visible at the 10-m level, were present at depth.

Bigelow and Sears (1939) noticed a northwardly shift in the centre of population along the American continental shelf and considered that its direction would be that expected for a boreal species, with the seasonal warming of waters. They also witnessed a southwardly shift in the early autumn. Similar seasonal movements were shown in the present survey and are considered to be in part the result of vertical rather than horizontal migrations.

From late winter to mid-summer, specimens appeared in the surface waters according to a geographical progression

(sequence, Table 9; Figs. 22, 37-41). They occurred first in the south-western part of the Labrador Current and a few months later inhabited, as well, waters of the subarctic gyre and North Atlantic Drift. Possibly such a widespread and rapid extension of distribution might compare with horizontal transport by ocean currents. More likely, however, specimens which occurred at depth throughout the entire subarctic and Drift region, progressively ascended into the 10-m level as they were stimulated to do so. This progression seems more strongly related to a latitudinal effect, such as day-length during winter and spring, than to other influences such as the timing of summer warming or the temperature prevailing in winter and spring (Fig. 22), which may be modified according to the distribution of water masses.

By late autumn, while young specimens in southern parts of the Labrador Current and the Drift remained in surface waters, most of those in the subarctic gyre and colder North Atlantic Drift currents appear to have withdrawn. Despite the impression that the species had moved southward, it seems most likely that specimens at higher latitudes have merely migrated below the level of sampling. Presumably in the north, where the season of abundance ends sooner, the species would be triggered earlier to return to deeper levels. Whether the majority of adults or a large proportion of young suffer an early mortality or a gradual cropping by predation is unknown. From the appearance of maturing and new-born specimens in

spring and early summer, however, there is little doubt that a sufficient number survive the winter at depth.

Mackintosh (1934) found that the vertical distribution of Parathemisto gaudichaudii in the Antarctic varied little across the 100-m level. Kane (1966) showed that despite this diurnally consistent abundance in the top 100 m of this ocean, night collections in the upper 5 m generally exceeded day ones. She suggested that those animals within the surface water migrated downwards during the day. By avoiding capture no more at this time than at night, their total numbers in the water column were therefore similar between night and day.

Bousfield (1951) found that in the region of Belle Isle Strait, bispinosa was frequently more abundant at the surface than at 25 m during the day but relatively less numerous here at night. For compressa, on the other hand, the relative abundance between these depths differed little between night and day.

From the present survey it would seem that in surface waters the species is always more abundant at night than during the day, apparently exhibiting the same daily vertical migration shown by Kane (1966) for the species in the Antarctic. This diurnal difference in the North Atlantic appears to be more noticeable in some of the summer months (section F2.3) and particularly strong in a region where the Gulf Stream with its major meander to the north is expected to approach parts of the Labrador Current and

subarctic gyre (Fig. 20).

McLaren (1963) has suggested that the behaviour for diurnal vertical migration has an advantage for survival of the species. He proposes that the migration takes advantage of the gradient of temperature with depth and, points out that in general, decreased temperatures result in increased adult-size and increased generation-time and that with increased size, fecundity is exponentially greater. An animal feeding in warm surface water and resting in cooler (deeper) water then gains and "energy bonus" which may be put into fecundity.

The gradient of temperature with depth will be steeper where a warm water mass may override a cold one, particularly when surface waters are warmed in summer. Thus, the bonus might be obtained over a shorter vertical distance with less energy expended on migration. In such a situation, keen competition and consequently high selective pressure could possibly encourage a larger than usual proportion of the population to exercise the daily migrations, and further, to win the energy bonus and hence, to gain greater fecundity. This hypothesis suggests why in certain surface waters of the western North Atlantic, the ratio of night to day numbers was especially high (Fig. 20) and the proportion and abundance of younger specimens particularly great (Figs. 30c, 31, 33--cf. B6 and D8).

Not all specimens exhibited this diurnal withdrawal from the surface. The very young, particularly, persisted

at the 10-m level both day and night. Not until these had grown to medium size (Fig. 33 - night/day) and shown signs of morphological development (section F3.3) did they vacate this level during the day. Presumably, before specimens become capable of sustained daily migration, they must achieve a certain amount of growth and development.

H SUMMARY

1. Four years of monthly collection by the Continuous Plankton Recorder survey in the North Atlantic Ocean and North Sea have been examined to investigate the distribution and abundance of hyperiid amphipods.

2. At the 10-m level sampled by the survey, genus Parathemisto accounted for more than 95% of all specimens present. Other genera were poorly represented as would be anticipated from the low taxonomic diversity expected in a region dominated by the circulation of cold water.

3. The identity of the characteristic species of the North Sea and North Atlantic shores has been confused in the past; it is now shown to be Parathemisto gracilipes.

4. Parathemisto gaudichaudii, known to occur widely over the oceanic North Atlantic, is for the first time shown, by analysis of size composition and relative abundance, to have its strongest ecological affinity for certain subarctic water east of Labrador. Young were particularly numerous along the southern arc of the subarctic gyre, with highest densities occurring between 50 and 55°N on average but extending as far north as 60°N in summer and autumn. Further sampling will be necessary east of the Grand Newfoundland Banks to complete the survey and thus to determine the southern extent of the

distribution.

5. The ratio of numbers of the two forms of P. gaudichaudii (bispinosa and compressa) were found to vary geographically, possibly in relation to the distribution of water masses. Furthermore there is some evidence from the literature that the forms behave differently with respect to vertical distribution and seasonal appearance.

6. The systematic problems of separating young specimens into the species P. gaudichaudii and P. gracilipes, and into the forms bispinosa and compressa, were not tackled in the present study. Whereas modern methods of numerical taxonomy might overcome these difficulties, a greater understanding would follow a study of their growth which would depend on the ability to rear animals successfully in the laboratory.

7. Some morphological features said to distinguish P. gaudichaudii, P. gracilipes and P. abyssorum were found not to do so. The lack of distal setae on the basal part of the maxilliped was found to be diagnostic for P. abyssorum, a feature not used since Sars (1895). Keys have been constructed for identification of the North Atlantic species of Parathemisto and the forms of P. gaudichaudii.

8. The study, by showing the situation at the 10-m level, has suggested a number of biogeographical problems that might be examined by a programme of sampling at greater depths. In particular: a. How far is the pattern of abundance in near-surface waters repeated at greater depths? b. Does the

distribution of P. gaudichaudii extend southward in submerged water of subarctic origin? c. Does the bulk of P. gracilipes in the north-eastern Atlantic reside at greater depth than in the North Sea? d. Does the Mediterranean Intermediate Water regularly transport species, such as P. gracilipes, from shelf waters of the eastern North Atlantic toward the west?

9. The present study indicates that, though breeding occurs year-round in the North Atlantic, there is a general tendency for P. gaudichaudii to reproduce most actively in the warmer months. At this time mature or nearly mature animals appear, probably from greater depths, accompanied by offspring which become increasingly numerous. The effects of mortality and perhaps emigration from the sampled depth are seen first in the adults followed shortly afterward among the developing young.

10. From comparison of seasonal abundances, in the present data and in the literature, the timing of the reproductive cycle of Parathemisto would appear to vary geographically although a closer examination of size frequencies and maturity changes is required to support this suggestion. In the north (south of Iceland) initiation of spawning would appear to have been delayed, more likely in relation to some latitudinal function, such as day-length, than to temperature which, being strongly associated with the distribution of water types, changes very little. In the south (south-west of Britain) breeding would seem to have been suppressed in mid-summer, possibly due to excessively high temperatures.

11. Though massive swarms containing breeding P. gaudichaudii were observed twice in the North Sea (where the species is usually rare or absent), sampling at the 10-m level failed to detect more than the normal scattered occurrences. There is evidence to suggest that in the North Sea this phenomenon may take place near the bottom (J.S. Gray, personal communication).

12. A programme of sampling to greater depth is necessary for information concerning growth and mortality of P. gaudichaudii during the overwintering period and is absolutely essential for any understanding of the seasonal abundance of P. gracilipes in relation to what is known of its breeding cycle (Evans, 1968b).

13. The distributions of taxa regularly occurring in the CPR survey were classified according to the water masses with which they appeared most closely affiliated. Communities geographically associated with P. gracilipes and P. gaudichaudii were thus revealed.

14. It was not possible to investigate directly the kinds of food consumed by Parathemisto sp. as the guts of animals caught in the sampler would be emptied by the mechanism for continuous recording. As those organisms consumed must be among those associated in the plankton, possible feeding relationships might reasonably be considered, particularly in an area such as south-west of Iceland, where relatively few species are present. Here, where P. gaudichaudii is the

predominant hyperiid, the maximum growth in numbers of one organism was followed by the greatest increase of another. From this, a seasonal succession of available foods, competitors and prey is suggested. There is now an urgent need to discover the details of feeding cycles in which Parathemisto might form a link.

15. Specimens were always more abundant by night than by day. For P. gaudichaudii this diurnal difference was greatest in summer and in a region of the North Atlantic where (by the juxtaposition of Gulf-Stream and subarctic waters) the thermocline would be especially steep and where (as indicated by size composition and numbers) reproduction and survival was highest. McLaren (1963) suggests that diurnal vertical migration, a conspicuous feature of Parathemisto, provides selective advantage whereby an animal by feeding actively in the warm surface layer and resting at reduced metabolic rate in cooler water below can win an energy bonus and hence achieve greater fecundity. The present data tend to support this hypothesis.

16. The ellobiopsid parasite Thalassomyces marsupii was found on P. gaudichaudii and on P. gracilipes, a new host. Possibly because of loss of the fruiting body of the parasite due to damage in the sampler, only three specimens were recognized in the CPR material. This was insufficient to indicate the rate of infection or the distribution of a possible intermediate host (Vader and Kane, 1968).

17. An increase in abundance during 1964 occurred both in the North Sea off Scotland and in the Atlantic west of the British Isles. Examination of long-term fluctuations, such as by the CPR survey, might indicate whether similar changes in hyperiid numbers are a regular feature of these areas.

18. Annual changes were small in comparison with other changes, with abundance tending to increase from 1962 to 1964 and to drop in 1965. Nevertheless, as shown by fluctuations in the relative number of small and large specimens, more subtle changes may have been occurring in the population structure, such as might be associated with variations in the seasonal cycle from year to year. Only if studied in the long term, however, would the result of such observation become meaningful.

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